5-1991

The Demographic and Morphological Characteristics of Black Bears in the Smoky Mountains

Peter Kleppinger McLean

University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Peter Kleppinger McLean entitled "The Demographic and Morphological Characteristics of Black Bears in the Smoky Mountains." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Michael R. Pelton, Major Professor

We have read this dissertation and recommend its acceptance:

Edward Clebsch, David S. Etnier, Sandy Echternacht, Ralph W. Dimmick, Boyd L. Dearden

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Vice Provost
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THE DEMOGRAPHIC AND MORPHOLOGICAL CHARACTERISTICS
OF BLACK BEARS
IN THE SMOKY MOUNTAINS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Peter Kleppinger McLean

May 1991

DEDICATION

This dissertation is dedicated to John and Frank Craighead, Edward Abbey, Henry David Thoreau, Aldo Leopold, Paul Ehrlich, Annie Dillard, Roger Tory Peterson, John McPhee, Sue Hubbell, and others who have encouraged us to explore and appreciate the natural world. There is no greater gift.

> One final paragraph of advice: Do not burn yourselves out. Be as I am - a reluctant enthusiast...a part-time crusader, a half-hearted fanatic. Save the other half for yourselves and your lives for pleasure and adventure. It is not enough to fight for the land; it is even more important to enjoy it. While you can. While it is still there. So get out there and hunt and fish and mess around with your friends, ramble out yonder and explore the forests, encounter the grizz, climb the mountains, bag the peaks, run the rivers, breathe deep of that yet sweet and lucid air, sit quietly for a while and contemplate the precious stillness, that lovely, mysterious and awesome space. Enjoy yourselves, keep your brain in your head and your head firmly attached to the body, the body active and alive, and I promise you this much: I promise you this one sweet victory over our enemies, over those desk-bound people with their hearts in a safe deposit box and their eyes hypnotized by desk calculators. I promise you this: you will outlive the bastards. (Edward Abbey, 1986, The Earth Speaks)

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Several people read earlier drafts of all or portions of this paper. I thank Carol Ann Pala, Bill Stiver, Frank Teunissen van Manen, Steve Seibert, Ken Johnson, Jeff Keay, Steve Pozzanghera, Bruce Hastings, and Dave Garshelis for their insights and comments.

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Service, and John Collins of the North Carolina Wildlife Resources Commission provided the data on hard mast; Steve Pozzanghera contributed, in large part, to its analysis. John Collins, David Allen, Dennis Martin, Dave Carlock, Doug Scott, and their respective agencies supplied data on the fates of many of our bears.

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Lastly, but most importantly, I am indebted to my family for their support in this and other endeavors. This project would have been much less were it not for their love and patience.

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ABSTRACT

Data on age, sex, body measurements, survival, and reproductive condition were collected from 1702 black bears (*Ursus americanus*) trapped in the Smoky Mountains (SM), 1972-1989. The age structure suggested a lightly to moderately exploited bear population. Bears of Great Smoky Mountain National Park (GSMNP or Park) were significantly (P = 0.026) older (mean = 4.52 yr) than those of Cherokee National Forest (3.74 yr) but not those of Pisgah (3.86 yr) National Forest ($P \leq 0.076$). SM females had a mean minimum reproductive age of 4.2 yr, birth interval of 2.4 yr, and litter size of 2.0 cubs. The percentage of lactating females was significantly associated with age (X^2 = 20.6, 2 df, $P < 0.001$), and lactation rates were significantly related to white oak mast production (r^2 = 0.51, $P \leq 0.01$). The annual mortality rate was 26% and was lowest for Park bears (22%) and highest for those of the national forests (30%). Density ranged from 0.09 to 0.35 bears/km^2, and the intrinsic rate of growth (2-11%) indicated a slightly to moderately increasing population.

Both extrinsic and intrinsic factors govern the population. Food is the chief control of bear reproduction. Hunting mortality appears to regulate the bear population in the national forests, and male aggression and subsequent subadult dispersal govern bear

abundance of the less-exploited Park population. Given these factors, and the cumulative effects of inconsistent hard mast production, poaching, and a habitat threatened by the gypsy moth (Lymantria dispar), roads, and resort development, this bear population may be jeopardized.

Gender was associated with the bear's status (i.e., panhandler/wild) (panhandler: 60% male, wild: 54% male, P = 0.056). Wild male bears were significantly older than panhandler males (3.9 vs 2.9 yr, P = 0.0001); wild female bears were older than panhandler females (4.9 vs 3.7 yr, P = 0.004). Male and female panhandlers were significantly heavier than their wild counterparts ($P < 0.05$), and panhandler bears grew faster than wild bears. The number of lactating females was significantly associated with status ($P < 0.001$); 56% of the panhandler and only 33% of the wild females were lactating.

Panhandlers were more fertile and larger than wild bears likely reflecting the panhandlers' better access to and use of high-energy, human-made foods particularly during years of natural food shortage. Small amounts of these foods, the availability of which varies with panhandler bear management, appear to make differences in body size. Dispersal and the large home-range size of the males and subadults probably explain the propensity of these bears to become panhandlers. The above findings as well as differences in demographic characteristics among wild bears within the Smoky Mountains are further discussed as they relate to the nutritional qualities of the environment.

Neck and chest circumferences and total length were significant ($\underline{P} \leq 0.0001$) predictors of body weight. The predictive capabilities of these variables were reliable, especially at the low-to-mid range of bear weights. This predictive relationship should ease the collection of weight data on black bears in the Smoky Mountains.

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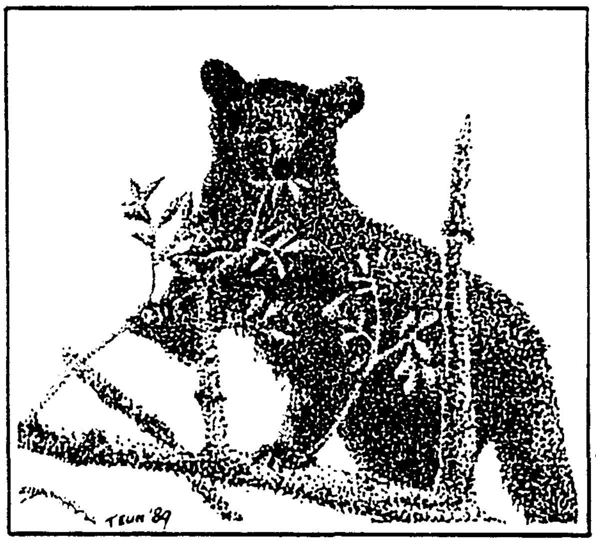

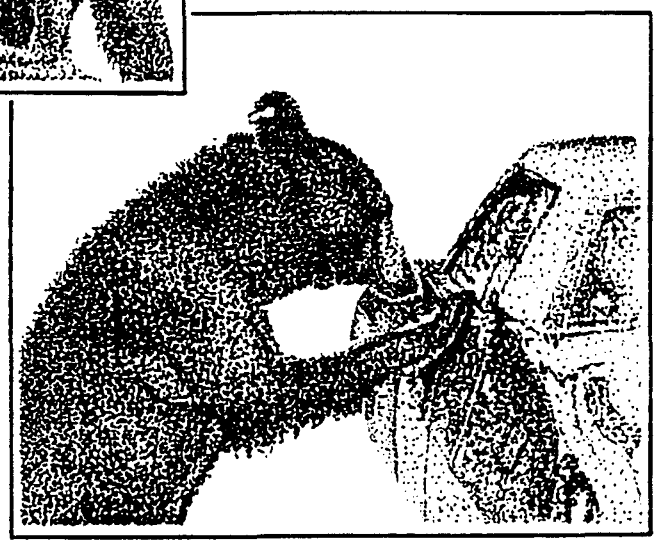

INTRODUCTION

Encroachment on ecosystems increases with growing resource needs of a burgeoning human population. For example, forests covered about one-fourth of the earth's land area in 1960, but, by the year 2000, they likely will cover only one-sixth (Harris 1984). We must delineate today's ecosystems to not only catalog what exists, but to track changes, both natural and human-influenced, over time.

Populations of animals, particularly large carnivores, are critical in maintaining the ecological integrity of ecosystems (Terborgh 1988) and can serve as indicators of their health (Mech 1970, Pelton and Beeman 1975, Craighead 1989). The status of animals at the top of the food chain reflects the well-being of animal and plant populations lower in the chain. If we can monitor the health of populations of animals at the top and, as a consequence, the ecosystem, then perhaps we can better manage our natural resources and, ultimately, ourselves.

From 1969 to 1989, research was conducted on the black bear, Ursus americanus, in the Smoky Mountains of Tennessee and North Carolina. During these years, Dr. Mike Pelton and a team of over 20 graduate students compiled a significant data base on this large mammal. Long-term studies of large, long-lived mammals are rare yet provide the only means to fully appreciate their population dynamics (Smith and Fowler 1981). The following 3 chapters represent an attempt to compile and synthesize this information, thereby improving our understanding of this black bear population and its changes over time. It also is hoped this analysis will function as a basis for future research on an animal that serves as an indicator of the health of the Smoky Mountains' ecosystem.

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PART I

THE POPULATION DYNAMICS OF BLACK BEARS IN THE SMOKY MOUNTAINS

INTRODUCTION

Habitat loss and fragmentation constitute considerable threats to wildlife populations (Dasmann 1981, Harris 1984). Black bears (*Ursus americanus*) have lost over 90% of their original range in the southeastern United States (Pelton 1986), and much of what remains lies in scattered tracts of public lands (Maehr 1984). Due to their sensitivity to habitat alterations, black bears are considered environmental indicators (Pelton and Beeman 1975). As such, and to ensure proper management, an understanding of their population dynamics is essential.

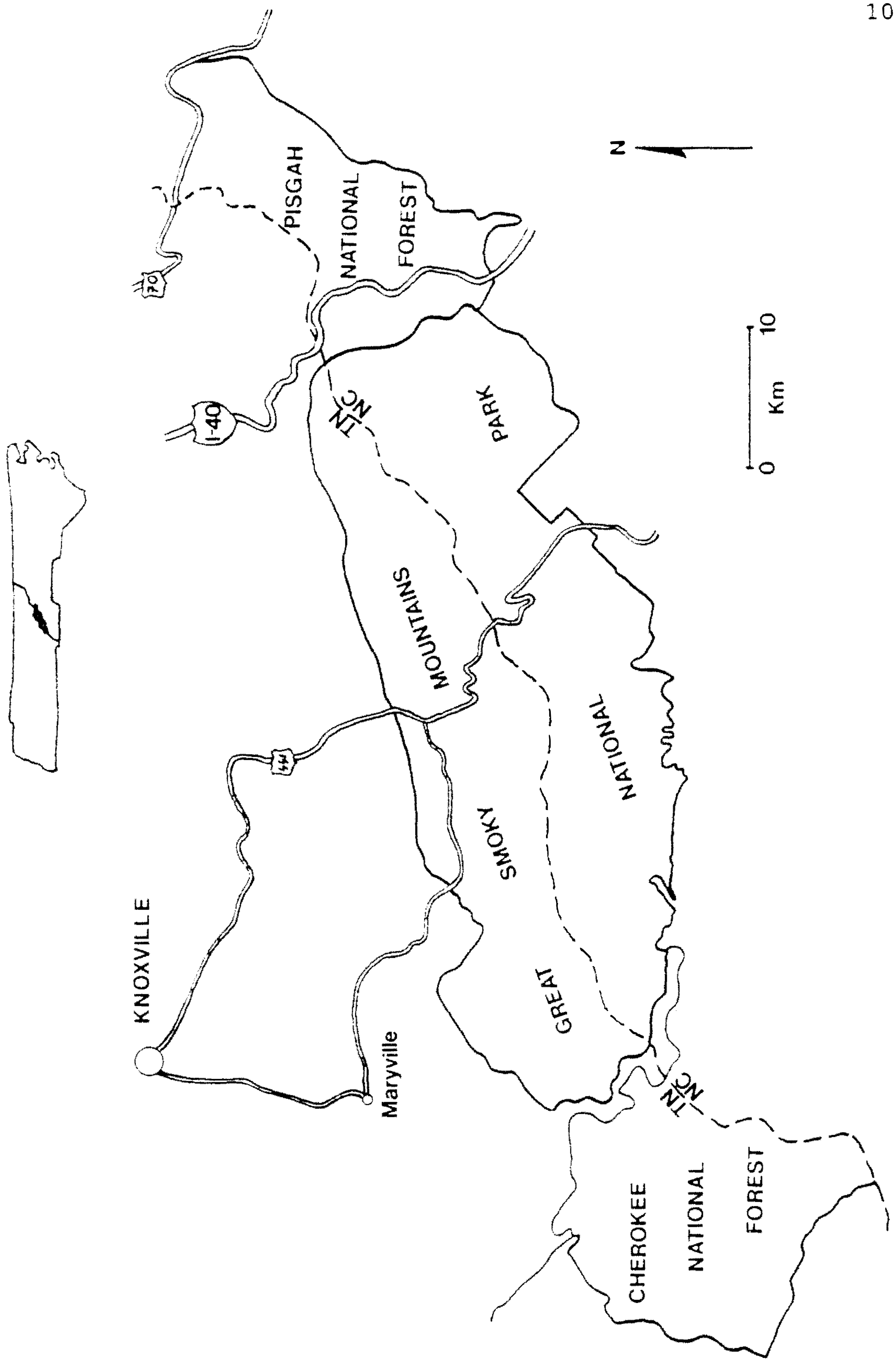
In portions of the Smoky Mountains (SM or Smokies), such as Cherokee (CNF) and Pisgah (PNF) National Forests, black bears are legally harvested though poaching is a significant source of mortality as well. In Great Smoky Mountains National Park (GSMNP or Park) legal harvest of bears has been prohibited for over 50 years, but poaching persists. To better understand the survival, movements, density, and reproduction of bears of these mountains, researchers have collected information for nearly 20 years. The purpose of this study is to assimilate the collected information and characterize this black bear population. Specifically, the objectives are to evaluate the population's age and sex structure, to estimate age-specific mortality and natality, abundance, and population growth, and to elucidate the principal factors controlling these characteristics over time.

STUDY AREA

Great Smoky Mountains National Park, visited by nearly 10 million people annually, is located in eastern Tennessee and western North Carolina (Fig. 1.1). Approximately 1/4 (506 km^2) of the Park, the northwest portion, served as one study area from 1968-1989. The Park is characterized by steep ridges, narrow valleys, coves, and fast-flowing streams (King and Stupka 1950). Elevation ranges from 230 to 2035 m (Pelton et al. 1980). Average temperatures vary from 14°C at low elevations to 8°C at high ones (Shanks 1954). Considered a temperate rain forest (Thornthwaite 1948), the Park receives 140 cm of annual precipitation at low elevations and 230 cm at high elevations (Stephens 1969). Six major forest types are recognized (Shanks 1954): cove hardwood, hemlock (Tsuga canadensis), northern hardwood, open oak-pine (Quercus spp.-Pinus spp.), closed oak, and spruce-fir (Picea rubens-Abies fraseri). Understory vegetation is dominated by mountain laurel (Kalmia latifolia), rhododendron (Rhododendron spp.), blueberries (Vaccinium spp.) and huckleberries (Gaylussacia spp.).

The Pisgah National Forest study area comprises 114 km^2 (Brody 1984) in western North Carolina (Fig. 1.1). This area, northeast of GSMNP, is similar to the Park in terms of climate and geology. Elevations commonly range from

Fig. 1.1. Location of Great Smoky Mountains National Park and Cherokee and Pisgah National Forests in eastern Tennessee (TN) and western North Carolina (NC).


PISGAH
NATIONAL
FOREST
70
I-40
TN
NC
PARK
N
0
Km
10
MOUNTAINS
NATIONAL
441
SMOKY
KNOXVILLE
GREAT
Maryville
TN
NC
CHEROKEE
NATIONAL
FOREST

439 to 1411 m (Beringer 1986). Of the nearly 2000 plant species identified in this national forest, several are predominant in the overstory including white (Quercus alba), northern red (Quercus rubra), scarlet (Quercus coccinea) and chestnut oaks (Quercus prinus), hickory (Carya spp.) and yellow-poplar (Liriodendron tulipifera); nearly 90% of the study area is in hardwoods with oak or oak-associates comprising 74% (USFS 1981 in Beringer 1986). In 1971, the area was designated as the Harmon Den Bear Sanctuary with hunting restricted to that of small game (excluding raccoon) and deer (Beringer 1986). The area's high road density provides easy access for hunters and other recreationists, and bear poaching within and around the sanctuary is a significant source of mortality. Logging operations, managed by the U. S. Forest Service, continue today though not with the same intensity of those of the early 1900's (Beringer 1986). The University of Tennessee has conducted black bear research in Pisgah National Forest since 1981.

To the southwest of the Park lies the Cherokee National Forest study area (Fig. 1.1). It is situated within the Tellico Ranger District, Tennessee, and constitutes about 760 km^2 (Clevenger 1986). It also is similar in geology and climate to that of the Park (Clevenger 1982). Elevations range from 450 to 1550 m, and the area is generally characterized by steep mountains and fast-flowing streams (Clevenger 1986). It is 99% forested with 5 major plant communities recognized: cove hardwood, northern hardwood, oak-hickory, pine, and mesic hemlock (Clevenger 1986). The forest cover was significantly altered by logging and associated fires until the Forest Service purchased the land in the 1930's (Clevenger 1986). A 124-km^2 segment of the study area serves as a bear refuge reserved for small game hunting (Clevenger 1986). Black bears were trapped in an approximate 80-km^2 portion of the study area. Black bear data were collected in the Cherokee study area from 1972-1983.

MATERIALS AND METHODS

Black bears were trapped June through September, 1972-1988. Trapping and marking techniques outlined by Johnson and Pelton (1980a,b) were employed, though barrel traps sometimes were used. Bears were sedated with a 20:10:2 mg/ml mixture of ketamine, rompun, and carbocaine; in the first years of the study, other immobilizing drugs were employed (Cook 1982). Bears were weighed with spring scales (300- and 500-lb capacity) to the nearest pound, and weights later were converted to kilograms. To age bears, the first premolar, a vestigial tooth, was extracted, sectioned, and stained (Eagle and Pelton 1978). Ages were assigned according to Willey (1974), and bears ≥3 yr were considered adults. The female bear's reproductive condition was evaluated via vulva and teat examination and the presence of young. Pitocin or oxytocin was administered to help detect lactation. Beginning in 1978, radio-collars were fitted to females enabling us to locate them in winter.

During winter, 1978-1989, the reproductive status of denning females was assessed. The presence of young was noted, and sonagram analysis sometimes was used to determine cub number (Wathen 1983).

The maximum percent production index (MPPI) (Pozzanghera 1990) and the Whitehead index (C. J.

Whitehead, oak mast yields on wildlife management areas in Tennessee, Tenn. Game and Fish, unpubl. rep., 11pp., 1969) (see Appendix A) were used to assess hard mast production. The MPPI is comparable to the Whitehead index but improves on its shortcomings; apparently, the calculation of the Whitehead index has no "biological rationale" (Nicholas and White 1984:23). Only the MPPI results are reported.

Field data were organized and statistically analyzed with the Statistical Analysis Systems procedures (SAS Institute 1985). Because within-year recaptures were low (<5%) and to incorporate all the data, recaptures were used in the analysis unless otherwise indicated; analysis using only individual bears was similar in terms of significant results (McLean unpubl. data; see part II). Where sample sizes for the national forest study areas were too small and the data for these areas were comparable, data were combined to make meaningful statistical comparisons. Reproductive rates were calculated by multiplying the percentage of lactating females by the average litter size for each age class (Stirling et al. 1980, Kolenosky 1990). Age of primiparity, based on evidence of lactation and/or presence of young, and birth interval were determined from reproductive histories. Mortality rates were figured from life table (Craighead et al. 1974, Caughley 1977) and capture analyses (Program Jolly, Pollock et al. 1989); the few drug- or trap-related mortalities were excluded from these analyses. Program Jolly generated population estimates for the study area. The intrinsic rate of population growth, r, was solved by using the equation, $\Sigma l_x e^{-rx} m_x = 1$ (Caughley 1977). Regression, correlation, and test of independence (Chi-square) were used to test the level of association between variables. The T-test or ANOVA served to compare means. Level of significance was determined at $\underline{P} = 0.05$.

Black bears of the Smokies likely belong to one population although some of the analysis may suggest otherwise. Emigration and immigration of bears among the study areas (Quigley 1982, Carr 1983) indicate a single population; long-distance movements, particularly by males, ensure gene flow between bears in the national forests and the Park. However, because management in the Park differs from that in the national forests, one might expect regional differences within the population; demographic features of Park bears might vary from those of the national forest. This analysis attempts to examine some of the possible differences.

To simulate the effects of hard mast on reproduction and population abundance, a population model composed of the Leslie matrix (Leslie 1945) and a component representing the stochastic variation in food supply (Mathis et al. 1991) was used. The Leslie matrix, among the simplest of population models, predicts population number using age- and sex-specific fecundity and survivorship rates. Alone, the predictions of the matrix must be interpreted broadly; however, in combination with other variables, such as vulnerability to hunting (Bunnell and Tait 1980) and food, the predictive capabilities of the model become more consistent with reality.

To represent the effects of food on the reproductive rates of females in GSMNP (see Table B.1), the model uses a series of multipliers. These multipliers are calculated based on the percentage of lactating females following good, bad, and average years of hard mast (Mathis et al. 1991); in GSMNP, 58%, 26%, and 42% of the females ≥5 yr were lactating following good, bad, and average mast years, respectively. Thus, the multiplier for good years becomes .58/.42 or 1.39; for bad years, the multiplier is .26/.42 or 0.62. In a good year, for example, the fecundity rate for females ≥15 yr (normally, 0.643 [taken from life table], see Table B.1) becomes (1.39)(0.643) or 0.894, and, in a bad year, the food-adjusted fecundity rate for these females is (0.62)(0.643) or 0.399. To account for delayed maturation due to food shortage (Eiler et al. 1989), the multiplier for 3-yr-old females is 0, except in good mast years (multiplier = 1.0). In bad mast years, fewer 4-yr-old females likely reproduce (Eiler et al. 1989) thus the multiplier for these females becomes 0.4; in good or average years the multiplier for these females is 1.0.

The percentages of lactating females in the NF following good, bad, and average years of mast were 0.757, 0.235, and 0.600, respectively. These values were used to calculate multipliers which, in combination with values of life history parameters of NF females (see Table B.2), produced food-adjusted fecundity rates.

The multipliers representing survival of females ≤4 yr are 1.25, 1.00, 0.75 representing good, average, and bad mast years, respectively. These multipliers reflect food-dependent cub survival as well as the fact that food availability affects the degree of social intolerance, dispersal, and, ultimately, survival of young bears (Garshelis and Pelton 1981).

RESULTS

Including summer captures and winter den visits, 1239 (605 individual) bears in the Smoky Mountains were handled. Most (*n* = 946) of these captures and visits were in Great Smoky Mountains National Park; 161 (81 individual) and 130 (60 individual) black bears were examined in Cherokee and Pisgah National Forests, respectively.

Sex and Age Structure

Sex ratio. Proportionally more males than females were captured especially in the younger (≤5 yr) age classes (Table 1.1). From year to year and by age group (subadult/adult), the sex ratio ranged from 40 to 65% male (mean = 55%, *n* = 569); the sex ratio was not associated significantly with the capture year (X^2 = 16.984, 16 df, *P* = 0.387). The sex ratio of adults was nearly equal (males 51%, *n* = 383), but there were more male (64%, *n* = 186) than female (36%, *n* = 103) subadults (X^2 = 15.036, 1 df, *P* < 0.0001).

The sex ratio did not vary significantly by study area; 52% (*n* = 312) of the Park adults, 51% (*n* = 43) of the CNF adults, and 43% (*n* = 26) of the PNF adults were males (X^2 = 1.516, 2 df, *P* = 0.469). Subadult males comprised 67% (*n* = 129) of those captured in the Park, 56% (*n* = 29) of those

Table 1.1. The age and sex structure of black bears in the Smoky Mountains, 1972-1988.

Age[a]	Sex	Percent (frequency)
0.5	M	56 (10)
	F	44 (8)
1	M	58 (46)
	F	42 (34)
2	M	68 (59)
	F	32 (28)
3	M	65 (73)
	F	35 (39)
4	M	68 (56)
	F	32 (27)
5	M	59 (29)
	F	41 (20)
6	M	43 (20)
	F	57 (27)
7	M	39 (13)
	F	61 (20)
8	M	45 (9)
	F	55 (11)
9	M	42 (5)
	F	58 (7)

Table 1.1 Continued.

Age	Sex	Percent (frequency)
10	M	60 (3)
	F	40 (2)
11	M	0 (0)
	F	100 (1)
12	M	0 (0)
	F	100 (4)
13	M	0 (0)
	F	100 (4)
14	M	0 (0)
	F	100 (3)
15	M	0 (0)
	F	100 (1)

[a]In years.

captured in CNF, and 62% ($\underline{n}$ = 28) of those captured in PNF (X^2 = 2.432, 2 df, $\underline{P}$ = 0.296).

Mean age. The mean age of captured bears was 4.36 yr (Table 1.2). Mean age of female bears (4.96 yr) was significantly ($\underline{P}$ = 0.0001) older than that of males (3.92 yr). In the Park, female bears (5.28 yr) were significantly ($\underline{P}$ = 0.0001) older than males (3.92 yr). However, the females (4.46 yr) in PNF were not significantly ($\underline{P}$ = 0.126) older than the males (3.33 yr). The mean age for SM males (4.32 yr) captured during the first half of the study, 1972-1979, was significantly ($\underline{P}$ = 0.011) greater than the mean age of males captured after 1979 (3.73 yr, Table 1.3); however, there was no significant ($\underline{P}$ = 0.490) difference in the mean age of females caught in the 70's (5.27 yr) versus those caught after 1979 (4.98 yr). In the Park, mean age for males caught in the 1970's (4.32 yr) was significantly ($\underline{P}$ = 0.019) greater than that of males caught in the 1980's (3.71 yr, Table 1.3); in the national forests, mean ages for males were not significantly ($\underline{P}$ = 0.296) different for the two periods (Table 1.3). Park bears (4.52 yr) were significantly ($\underline{P}$ = 0.026) older than those of CNF (3.74 yr) but not of PNF (3.86 yr, $\underline{P}$ = 0.076, Table 1.2). The oldest male and female bears were 15.5 and 22.5 yr, respectively.

Table 1.2. The mean ages of black bears[a] in Great Smoky Mountains National Park (GSMNP), Cherokee National Forest (CNF), and Pisgah National Forest (PNF), 1972-1988.

Area	Sex	Mean age[b]	SD	*n*
GSMNP	M	3.92	2.100	254
	F	5.28	3.224	183
	M+F	4.52	2.704	437
CNF	M	4.06	2.171	39
	F	3.28	1.761	27
	M+F	3.74	2.037	66
PNF	M	3.33	1.840	30
	F	4.46	3.256	26
	M+F	3.86	2.631	56
GSMNP+CNF+PNF	M	3.92	2.089	323
	F	4.96	3.155	236
	M+F	4.36	2.639	560

[a]Based on individuals, not recaptures.

[b]In years.

Table 1.3. The mean ages of black bears[a] in Great Smoky Mountains National Park (GSMNP) and Cherokee and Pisgah National Forests (NF), during the 1970's (1972-1979) and the 1980's (1980-1988).

		1970's			1980's		
Area	Sex	Mean age[b]	SD	n	Mean age	SD	n
GSMNP	M	4.32	2.374	130	3.71	1.649	119
	F	5.50	3.155	86	5.49	3.178	88
NF	M	4.33	1.800	23	3.78	2.099	40
	F	3.97	1.642	15	3.82	2.969	38
GSMNP+NF	M	4.32	2.292	153	3.73	1.766	159
	F	5.27	3.023	101	4.98	3.199	126

[a]Based on individuals.

[b]In years.

Proportion of adults. The proportion of adults, which was usually >50% annually (Fig. 1.2), was significantly associated with the years of capture (X^2 = 56.595, 16 df, P = 0.0001) and the study area (X^2 = 24.984, 2 df, P = 0.0001). The percentage of adults was greatest in the Park (76%, n = 605), followed by CNF (62%, n = 85) and PNF (57%, n =60) (Table 1.4).

Reproduction

Estrus. Female bears exhibited signs of estrus between 5 June and 19 September (106 days, Fig. 1.3). Most (75%, n = 63) were in estrus 15 June - 15 August, and only 3 (3.6%) females were in estrus in September. Those females in estrus 15 June - 15 August (6.08 ± 3.46 yr, n = 63) were significantly (P < 0.001) older than the females exhibiting estrus after 15 August (3.29 ± 0.893 yr, n = 14).

Minimum reproductive age and interbirth interval. The mean minimum reproductive age determined from the reproductive histories of 21 females was 4.24 ± 1.044 yr (n = 21). Six (28.6%) females were either lactating or with young as early as age 3; 5 of the 6 were handled in CNF or PNF. The mean minimum reproductive age for Park females was 4.82 ± 0.982 yr (n = 11), which were significantly (P =

Fig. 1.2. The number (frequency) of subadult and adult black bears captured in the Smoky Mountains, 1972-1988.

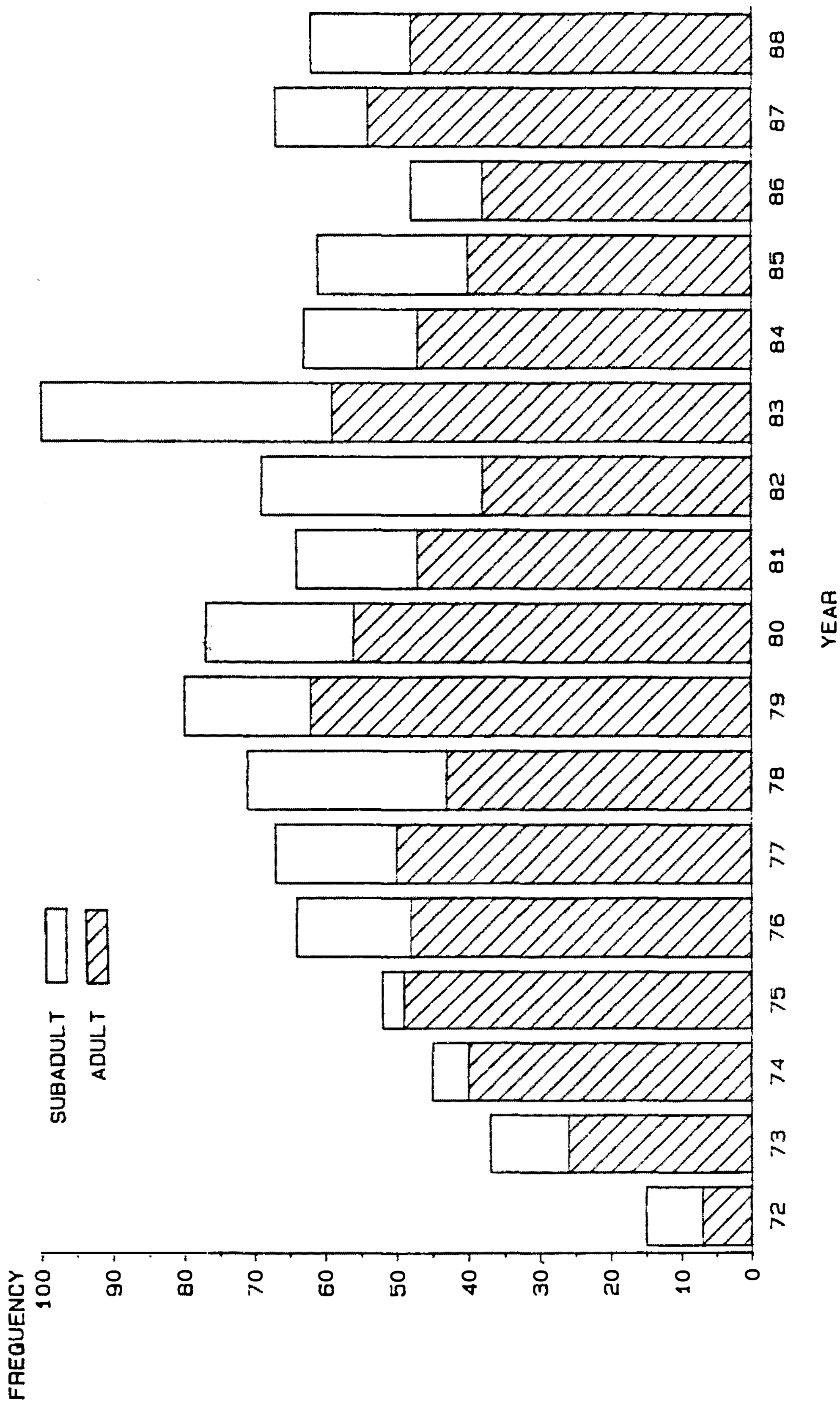
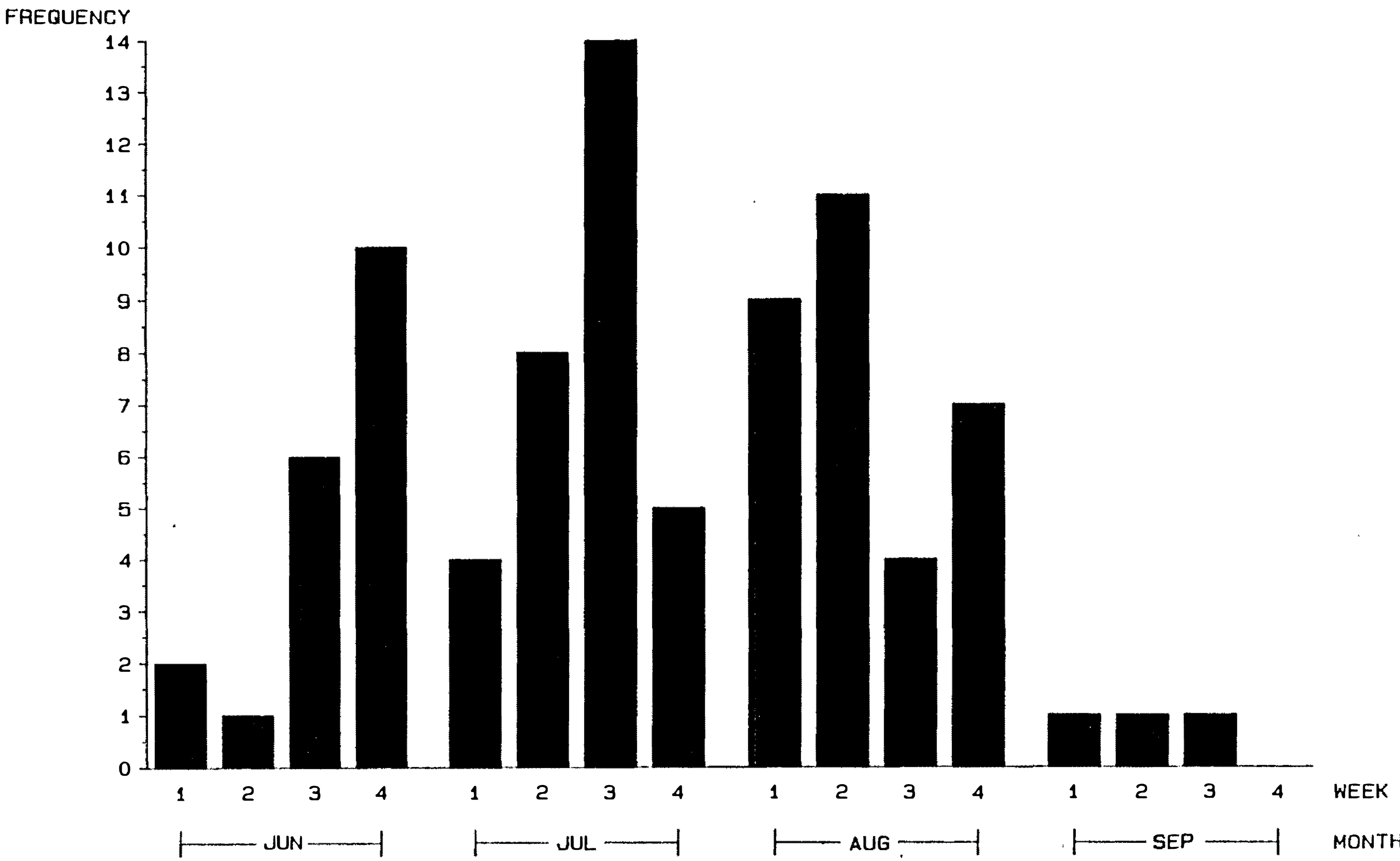

FREQUENCY
100
90
80
70
60
50
40
30
20
10
0
SUBADULT
ADULT
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
YEAR

Table 1.4. The percentage of subadult and adult black bears captured in Great Smoky Mountains National Park (GSMNP), Cherokee National Forest (CNF), and Pisgah National Forest (PNF), 1972-1988.

Age class	GSMNP	CNF	PNF
Adult	76 (605)[a]	62 (85)	57 (60)
Subadult	24 (193)	38 (52)	43 (46)

[a]Frequency.

Fig. 1.3. Seasonal distribution of observed estrus in female black bears in the Smoky Mountains, 1972-1988 (frequency = no. of bears).


FREQUENCY
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
1 2 3 4 1 2 3 4 1 2 3 4 1 2 3 4 WEEK
JUN JUL AUG SEP MONTH

0.004) older than national forest (NF) females (3.60 ± 0.699 yr, _n_ = 10; Table 1.5).

The mean birth interval determined from the reproductive histories of 23 females was 2.35 yr. The mean interval was 2.39 yr (_n_ = 18) and 2.20 yr. (_n_ = 5) for Park and NF females, respectively.

Litter size. The mean litter size was 2.04 cubs (range 1-4, _n_ = 114) and 1.94 (range 1-3, _n_ = 34) yearlings (Table 1.5). The mean litter size of Park females was 1.96 cubs (_n_ = 81) and 1.96 yearlings (_n_ = 23), and that of NF females was 2.25 cubs (32) and 1.91 yearlings (_n_ = 11); this difference was not significant (_P_ = 0.278).

Reproductive rate and lactation. By year, reproductive and lactation rates of females in the Smokies averaged 0.672 (range 0-1.539) and 33% (_n_ = 146) (range 0-100), respectively (Figs. 1.4 and 1.5). The mean weights of adult females did not vary significantly by age (_P_ = 0.415; Table 1.6). By age class, the reproductive rate of bears in the national forests (1.18 ± 0.444, _n_ = 8) was significantly (_P_ = 0.049) greater than that for bears in the Park (0.76 ± 0.428, _n_ = 13).

The percentage of lactating females was significantly associated with age (X^2 = 20.653, 2 df, _P_ < 0.001, Table 1.6). Fifty one percent (_n_ = 39) of the old (≥10 yr)

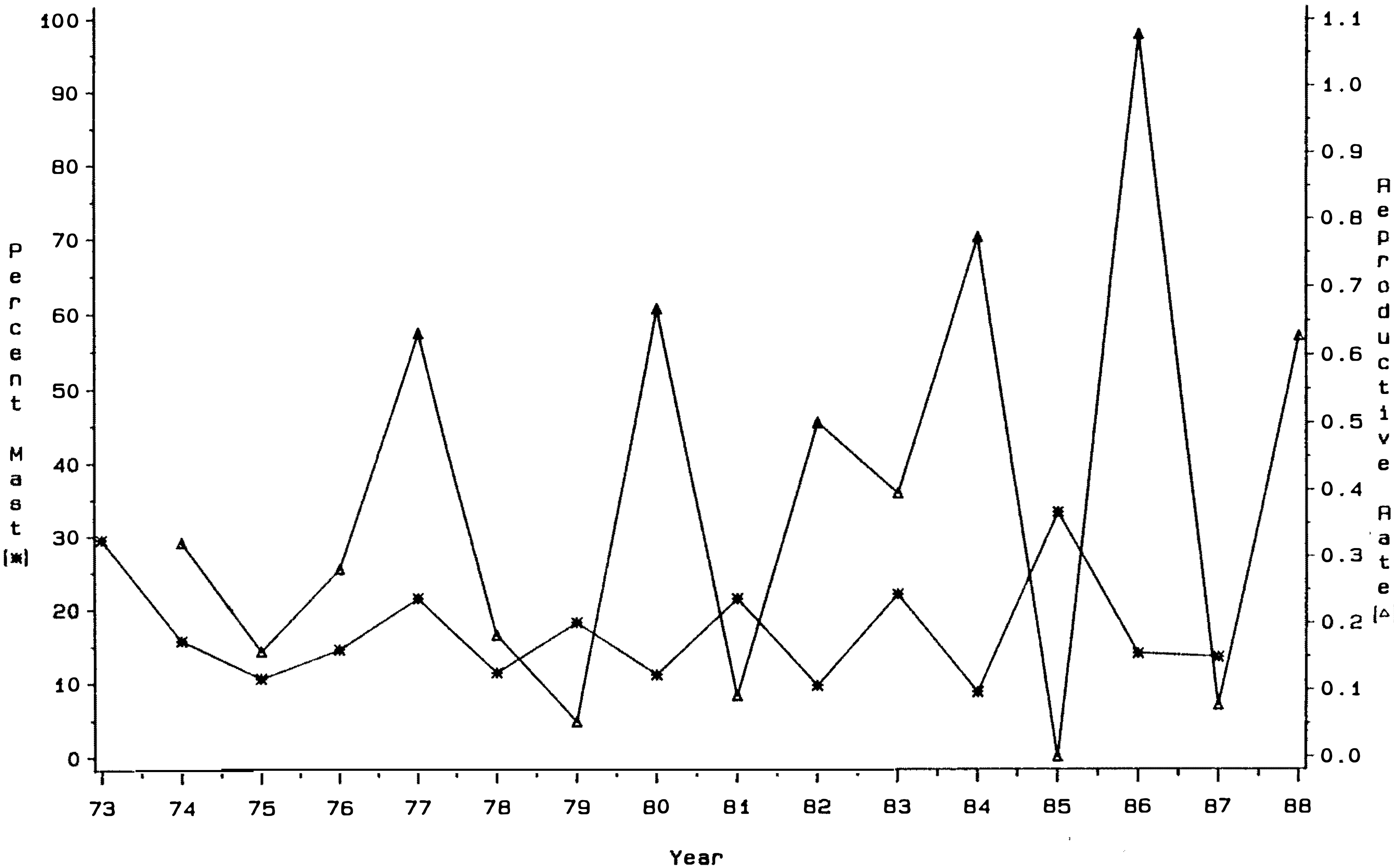
Table 1.5. The ages (yr) of first reproduction and litter sizes (cubs) of female black bears in Great Smoky Mountains National Park (GSMNP) and Cherokee and Pisgah National Forests (NF), 1972-1988.

	Age of first reproduction				Litter size			
Area	3	4	5	6	1	2	3	4
GSMNP	1[a] (9)[b]	3 (27)	4 (36)	3 (27)	23 (28)	40 (48)	18 (22)	2 (2)
NF	5 (50)	4 (40)	1 (10)	0 (0)	7 (21)	14 (41)	11 (32)	2 (6)

[a]Frequency.

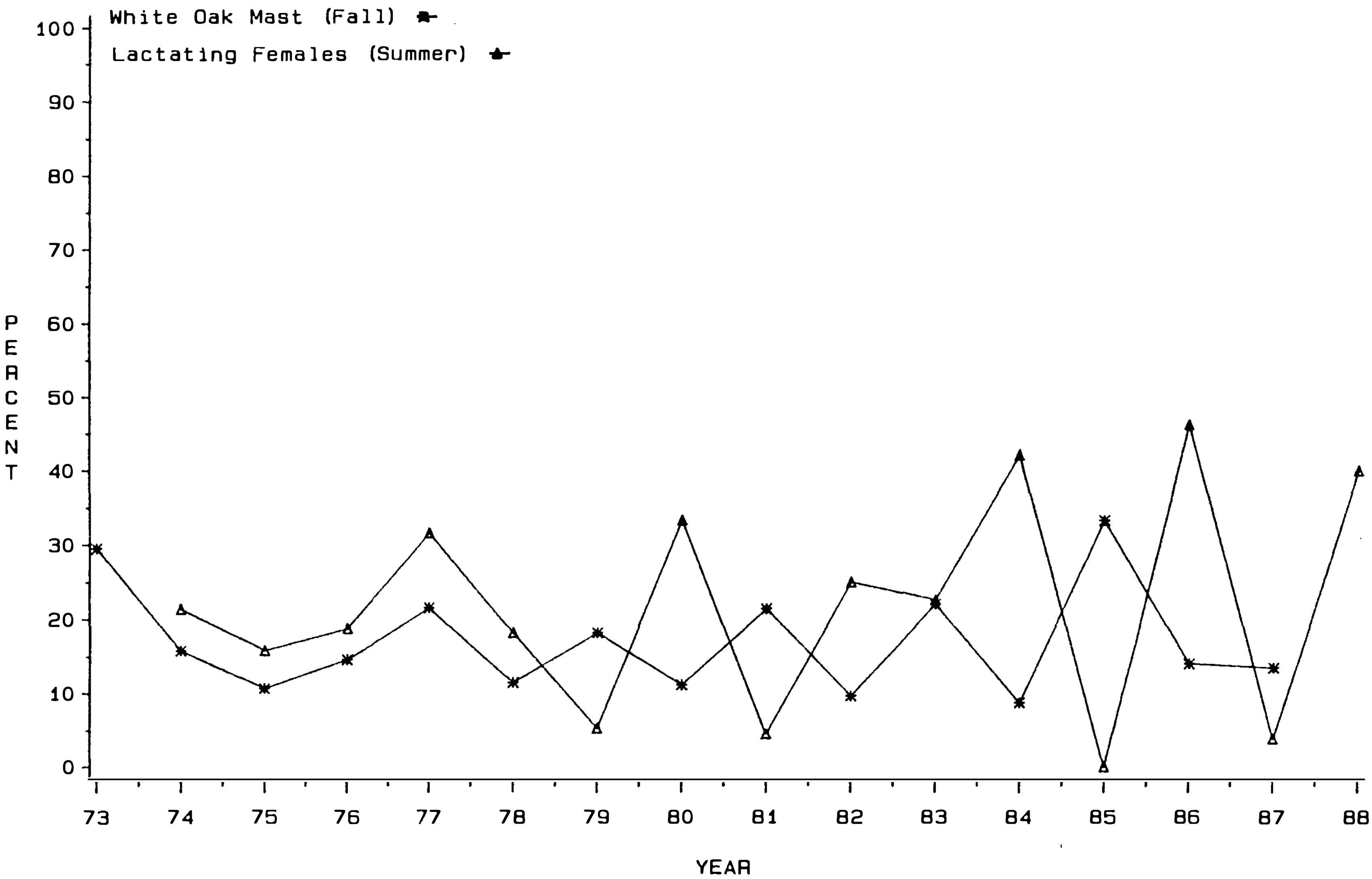
[b]Percent.

Fig. 1.4. Yearly fluctuations in white oak mast production and the reproductive rates of lactating black bears in the Smoky Mountains in the summer.



Percent Mast (*)
Reproductive Rate (Δ)
Year
0
10
20
30
40
50
60
70
80
90
100
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
1.1
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88

Fig. 1.5. Yearly fluctuations in white oak mast production and the percentage of lactating black bears in the Smoky Mountains in the summer.



White Oak Mast (Fall)
Lactating Females (Summer)
PERCENT
100
90
80
70
60
50
40
30
20
10
0
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
YEAR

Table 1.6. Mean weights (kg) and reproductive values of female black bears handled in the Smoky Mountains, 1972-1989.

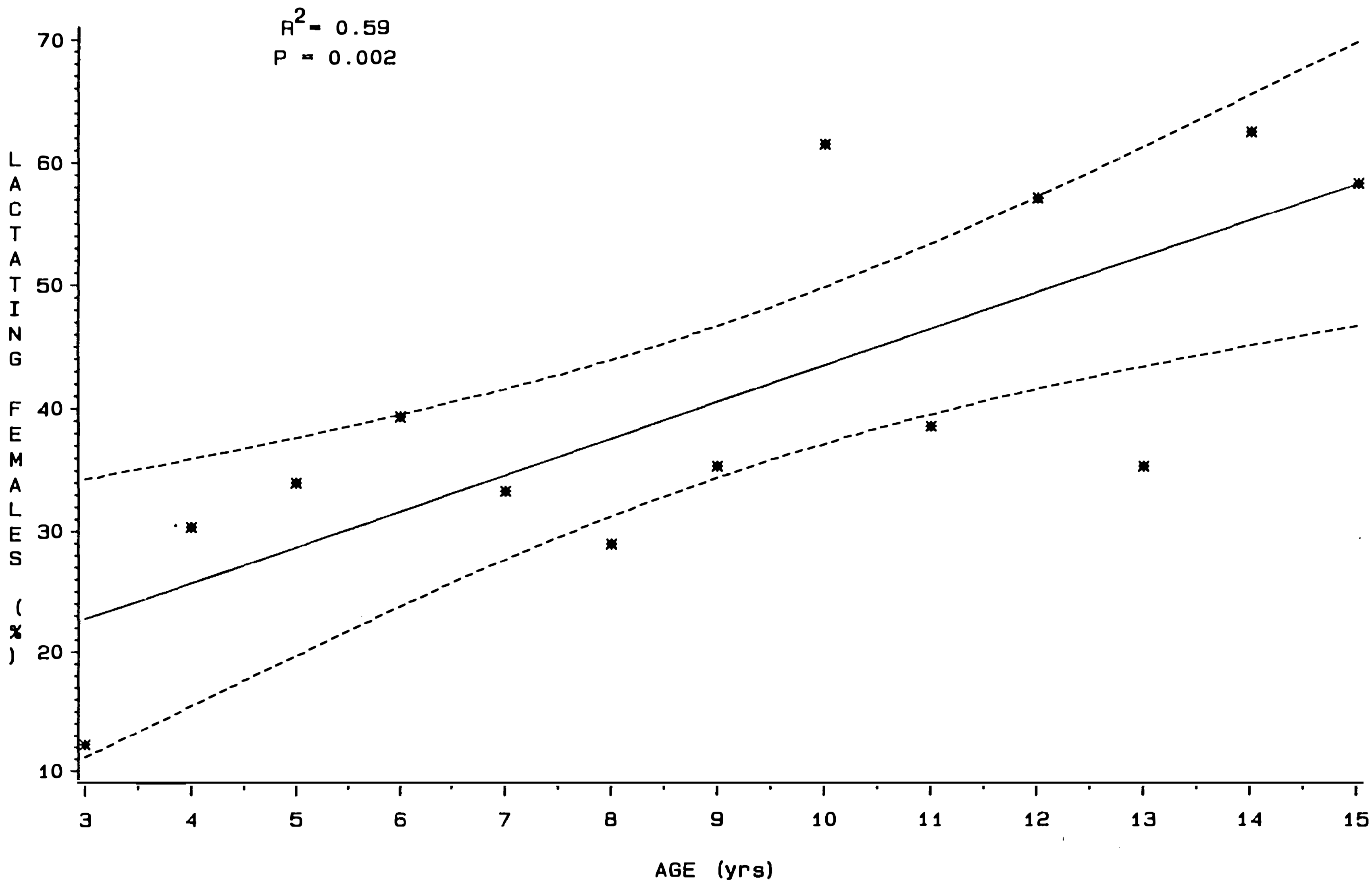
Age	Mean weight(SD, n)	Percent lactating (n)	Mean litter size (n)	Reproductive rate
3	40.1[a] (7.86, 63)	12.2 (9)	2.44 (9)	0.297
4	47.1 (9.90, 47)	30.3 (20)	1.80 (15)	0.545
5	49.3 (10.53, 39)	34.0 (18)	1.58 (12)	0.537
6	48.6 (9.67, 45)	39.3 (24)	1.76 (17)	0.694
7	50.0 (12.66, 42)	33.3 (19)	2.00 (16)	0.666
8	53.1 (9.56, 26)	28.9 (11)	2.38 (8)	0.688
9	54.5 (12.94, 14)	35.3 (6)	2.20 (5)	0.776
10	57.7 (7.33, 7)	61.5 (8)	2.40 (5)	1.477
11	52.3 (6.54, 8)	38.5 (5)	1.75 (4)	0.673
12	62.4 (11.74, 10)	57.1 (8)	2.50 (6)	1.428
13	56.3 (6.30, 10)	35.3 (6)	2.00 (5)	0.706
14	61.4 (11.63, 6)	62.5 (5)	2.25 (4)	1.406
15+	60.8 (22.5, 7)	58.3 (7)	2.57 (7)	1.500

females, and 34% (n = 78) of the middle-aged (5-9 yr), and 21% (n = 29) of the young (3-4 yr) females were lactating. Age (r^2 = 0.59, P = 0.002, Fig. 1.6), weight (r^2 = 0.79, P = 0.0001), and age and weight together (r^2 = 0.80, P = 0.0004) were significant predictors of lactation rates.

The percentage of lactating females also varied by study area. Forty-five percent (n = 18) of the young NF females and only 11% (n = 11) of the young Park females were lactating (X^2 = 20.111, 2 df, P = 0.001). Among middle-aged females, 51% (n = 18) of the NF bears and 31% (n = 60) of the Park bears were lactating (X^2 = 5.243, 1 df, P = 0.02). Among the old females, 71% (n = 5) of the NF bears and 49% (n = 34) of the Park bears were lactating, but small sample sizes from the national forests precluded any statistical comparison.

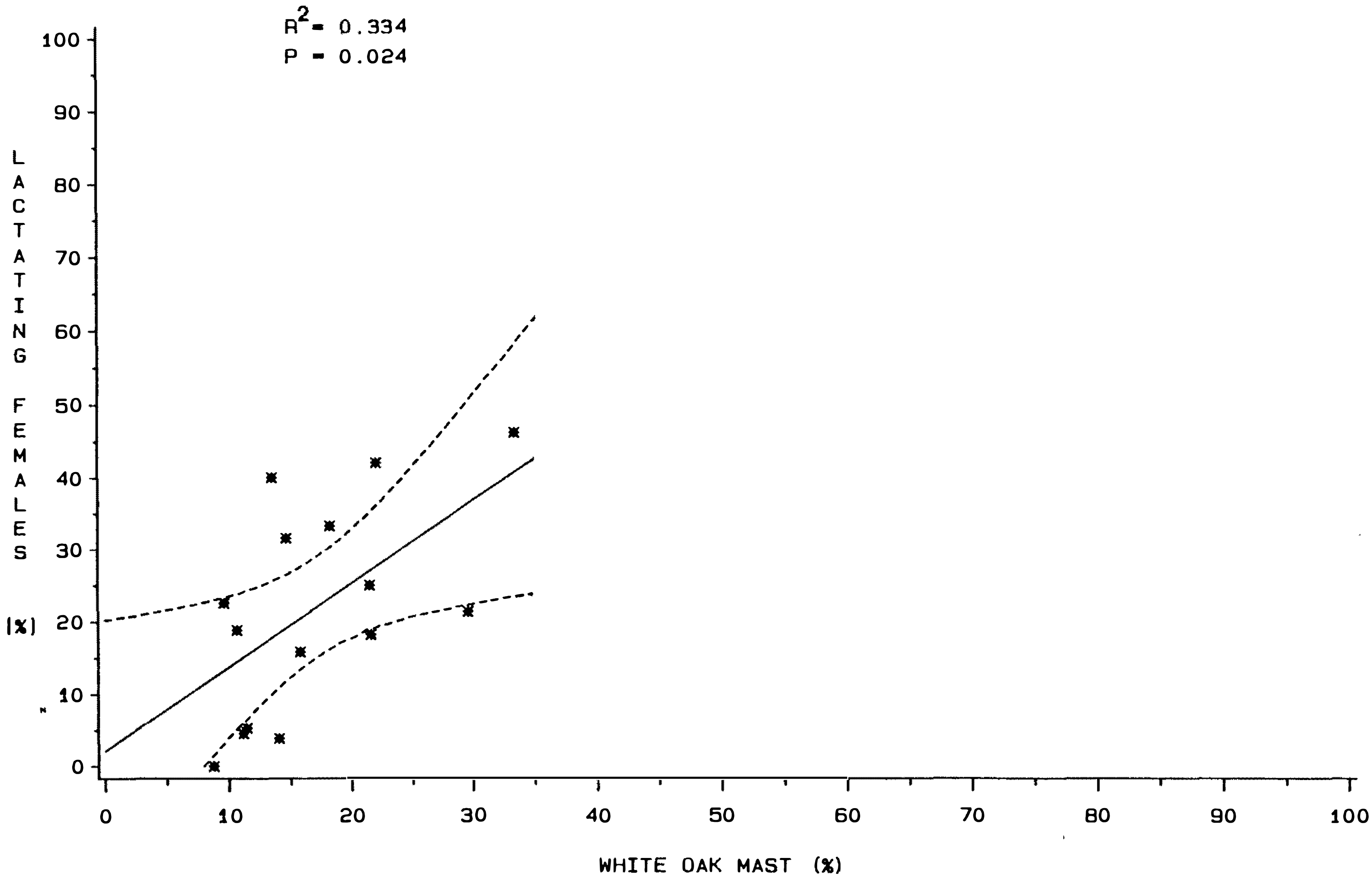
Hard mast and reproduction. Hard mast, particularly white oak mast, was a significant predictor of reproduction. White oak mast was a significant predictor of summer (r^2 = 0.334, P = 0.024, Figs. 1.5 and 1.7), winter (r^2 = 0.643, P = 0.002), and summer-winter (r^2 = 0.511, P = 0.013) lactation rates; it was also a significant predictor of summer (r^2 = 0.364, P = 0.017, Fig. 1.4), winter (r^2 = 0.549, P = 0.006), and summer-winter (r^2 = 0.428, P = 0.017) reproductive rates. Red oak mast was not significantly ($P \geq$ 0.07) associated with reproduction, but red and white oak

Fig. 1.6. Regression of the percentage of lactating black bears ($\underline{n}$ = 146) in the Smoky Mountains on age ($Y = 13.836 + 2.963x$).



R^2 = 0.59
P = 0.002
LACTATING FEMALES (%)
70
60
50
40
30
20
10
3
4
5
6
7
8
9
10
11
12
13
14
15
AGE (yrs)

Fig. 1.7. Regression of the percentage of lactating black bears (_n_ = 146) in the Smoky Mountains on the percentage of white oak mast production ($Y = 2.136 + 1.160x$).



R^2 = 0.334
P = 0.024
LACTATING FEMALES (%)
WHITE OAK MAST (%)
0
10
20
30
40
50
60
70
80
90
100

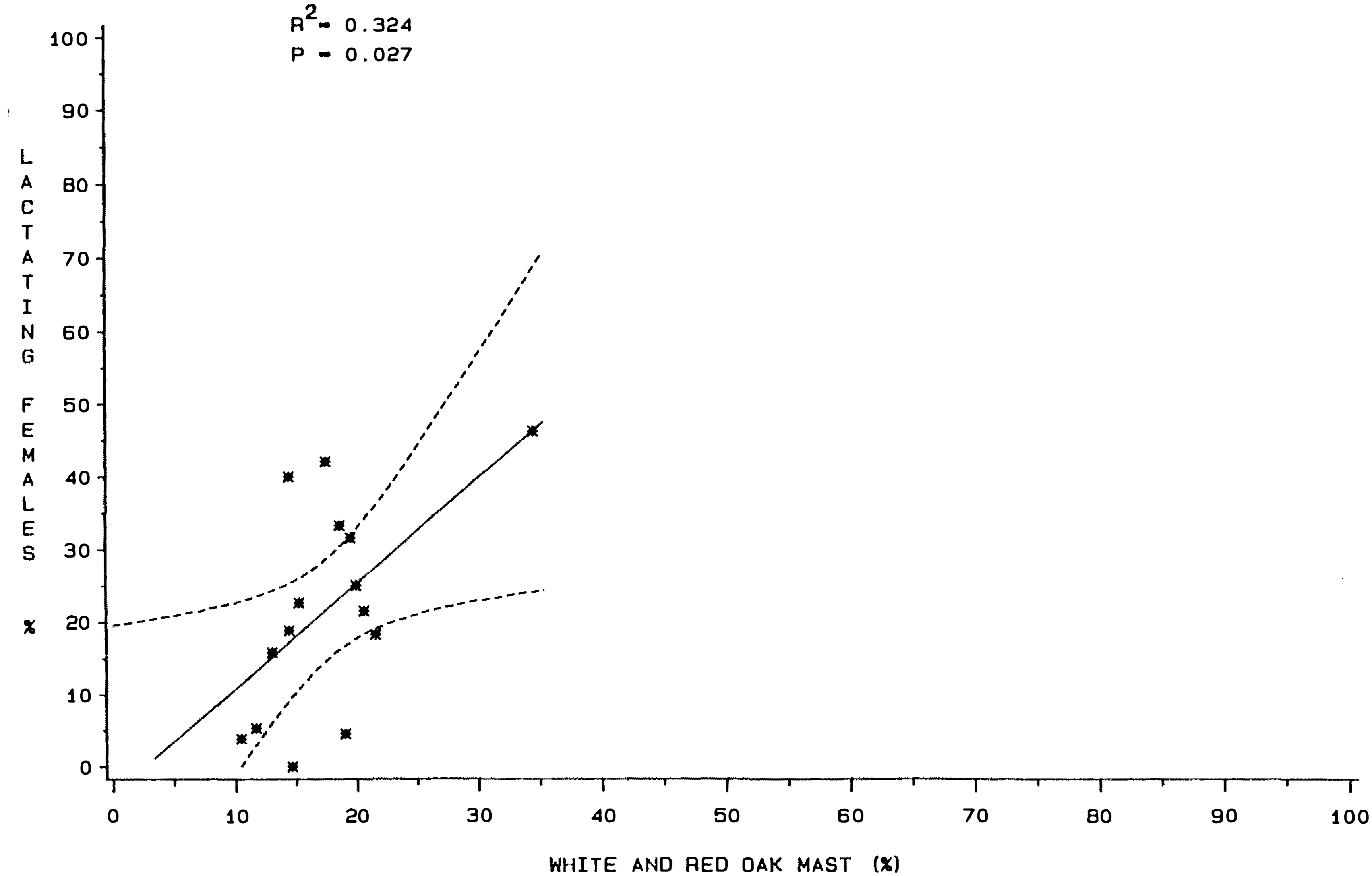
mast together indicated a significant or near significant linear relationship with summer (r^2 = 0.324, *P* = 0.027, Fig. 1.8), winter (r^2 = 0.257, *P* =0.092), and summer-winter (r^2 = 0.293, *P* = 0.085) lactation rates, and with summer (r^2 = 0.453, *P* = 0.006), winter (r^2 = 0.250, *P* = 0.098) and summer-winter (r^2 = 0.327, *P* = 0.066) reproductive rates.

Mortality

From 1972 to 1988, 110 mortalities were recorded (Table 1.7). Most (62%, *n* = 68) of these mortalities were males and 70% (*n* = 77) were adults. Fifty-nine percent (*n* = 65) of the deaths were Park bears. Six snared bears, 4 of which were subadults, were killed by other bears (Table 1.7). Sixty-one percent (*n* = 17) of recorded cub mortalities occurred in 1982.

Mortality rate. The annual mortality rate was approximately 26% for bears of the Smokies. Annual mortality rates were lowest for subadults (23%) and highest for cubs (28%). Adults had 27% annual mortality. Mortality rates were greater for males (29%) than females (22%). Mortality was lower for bears in the Park (22%) than for NF bears (30%). Cubs in the Park (35%) and NF adults (36%) had the greatest mortality; Park subadults (19%) and adults (20%) and NF subadults (24%) and cubs (25%) had the least. Park male (21%) and female (23%) mortality rates were nearly

Fig. 1.8. Regression of the percentage of lactating black bears (*n* = 146) in the Smoky Mountains on the percentage of white and red oak mast production ($Y = -3.725 + 1.457x$).



R^2 = 0.324
P = 0.027
LACTATING FEMALES %
WHITE AND RED OAK MAST (%)
0
10
20
30
40
50
60
70
80
90
100

Table 1.7. Mortalities of marked black bears in Great Smoky Mountains National Park (GSMNP), Cherokee National Forest (CNF), and Risgah National Forest (PNF), 1972-1989.

Cause	GSMNP[a]		CNF + PNF[a]		GSMNP+CNF+PNF[a]	
	n	%	*n*	%	*n*	%
Legal kill	32	49	33	73	65	59
Illegal kill	8	12	7	16	15	14
Killed by another bear	6	9	-	-	6	5
Road kill	3	5	1	2	4	4
Drug- or trap-related	2	3	4	9	6	5
Natural	3	5	-	-	3	3
Unknown	11	17	-	-	11	10
Total	65	100	45	100	110	100

[a]Originally marked in this study area.

equal, and NF males (36%) had a higher mortality rate than NF females (27%).

Although annual mortality rates produced from capture analysis (Program Jolly) were substantially higher than those calculated from life history tables, the trends were the same. Annual mortality for Park bears (27%) was lower than that for NF bears (41%). Annual mortality for subadults in the Smokies was 72%.

Population Size and Stability

Density. Estimates of density varied within the study area. From 1973-1987, the average population estimate for the Park study area was 148 ± 52.6 bears (Table 1.8) or 0.292 bears/km². During the first half of the study (1972-1979), the estimated size of the Park population was 123 ± 32.5 bears (n = 7 yr) or 0.243 bears/km², and from 1980 to 1988, this estimate rose to 170 ± 61.9 bears (n = 8 yr) or 0.336 bears/km² (Fig. 1.9); these estimates are not significantly different (P = 0.085). The population estimate for the CNF study area was 28 ± 13.8 bears (n = 6 yr, Table 1.8) or 0.350 bears/km², and the PNF study area was estimated to have 24 ± 6.5 bears (n = 5 yr) or 0.211 bears/km².

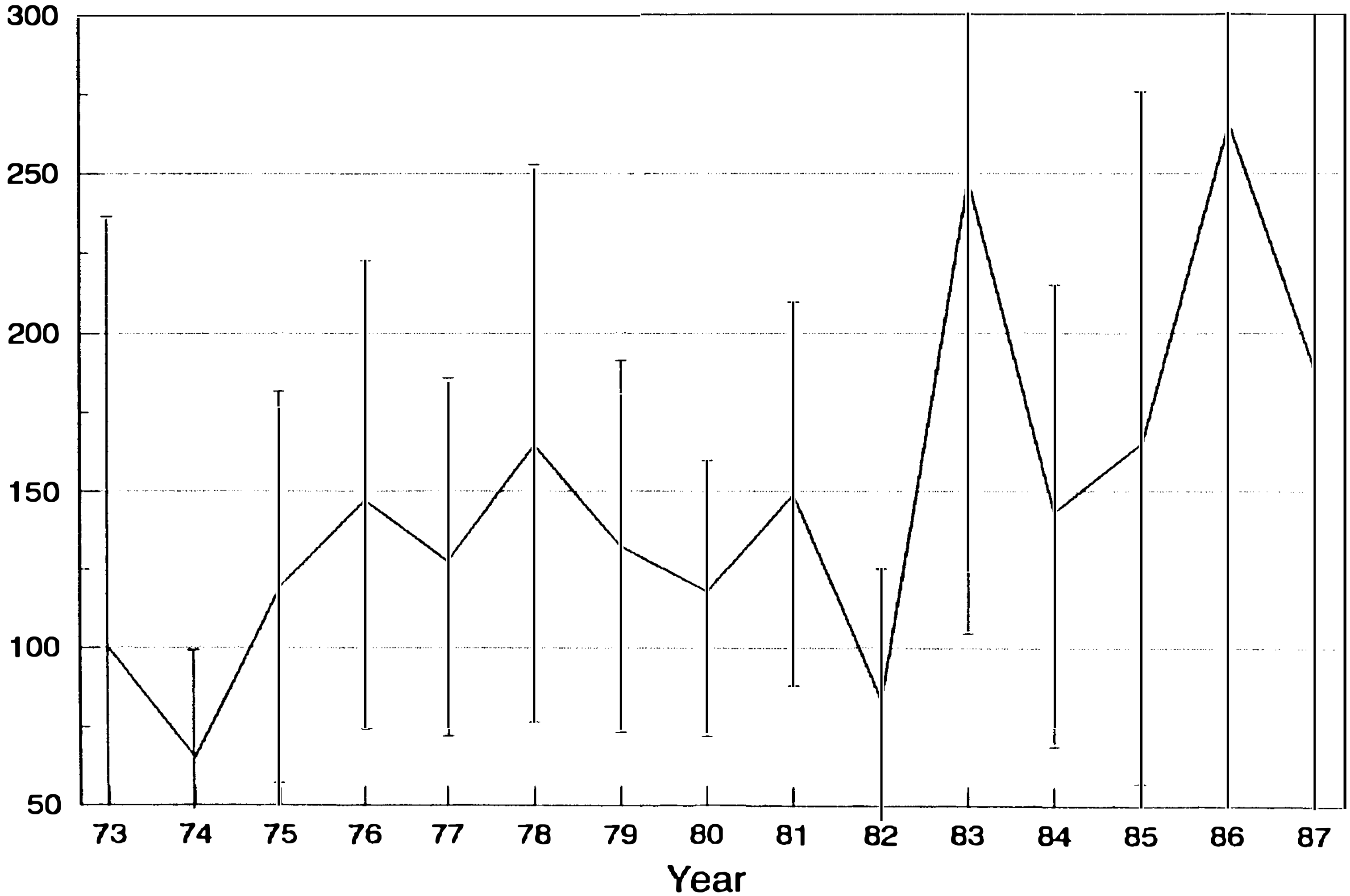
The estimated density of bears in the Park was correlated with the number of bears legally harvested in

Table 1.8. Jolly-Seber (Program Jolly) population estimates for black bears in the Smoky Mountains, 1973-1987.

	GSMNP	CNF	PNF
Year	_n_ (95% CI)	_n_ (95% CI)	_n_ (95% CI)
1973	100.1 (-33-233)	-	-
1974	65.4 (31-99)	-	-
1975	119.8 (58-181)	-	-
1976	147.4 (77-218)	-	-
1977	127.8 (72-183)	-	-
1978	165.0 (79-251)	15.0 (-)	-
1979	132.6 (77-188)	24.5 (-)	-
1980	118.0 (76-160)	46.2 (-)	-
1981	149.1 (87-211)	45.5 (-)	-
1982	83.9 (43-125)	19.5 (-)	-
1983	247.7 (107-388)	20.0 (-)	20.9 (7-35)
1984	143.5 (69-217)	-	28.6 (-8-65)
1985	165.4 (56-275)	-	27.0 (-7-61)
1986	265.7 (10-521)	-	12.0 (-)
1987	187.5 (37-338)	-	29.2 (-32-91)
Mean (SD):	147.9 (52.62)	28.4 (13.81)	23.5 (6.48)

Fig. 1.9. Annual fluctuations in the number of black bears in Great Smoky Mountains National Park, 1973-1987, based on Jolly-Seber population estimates.

Number of Bears in GSMNP

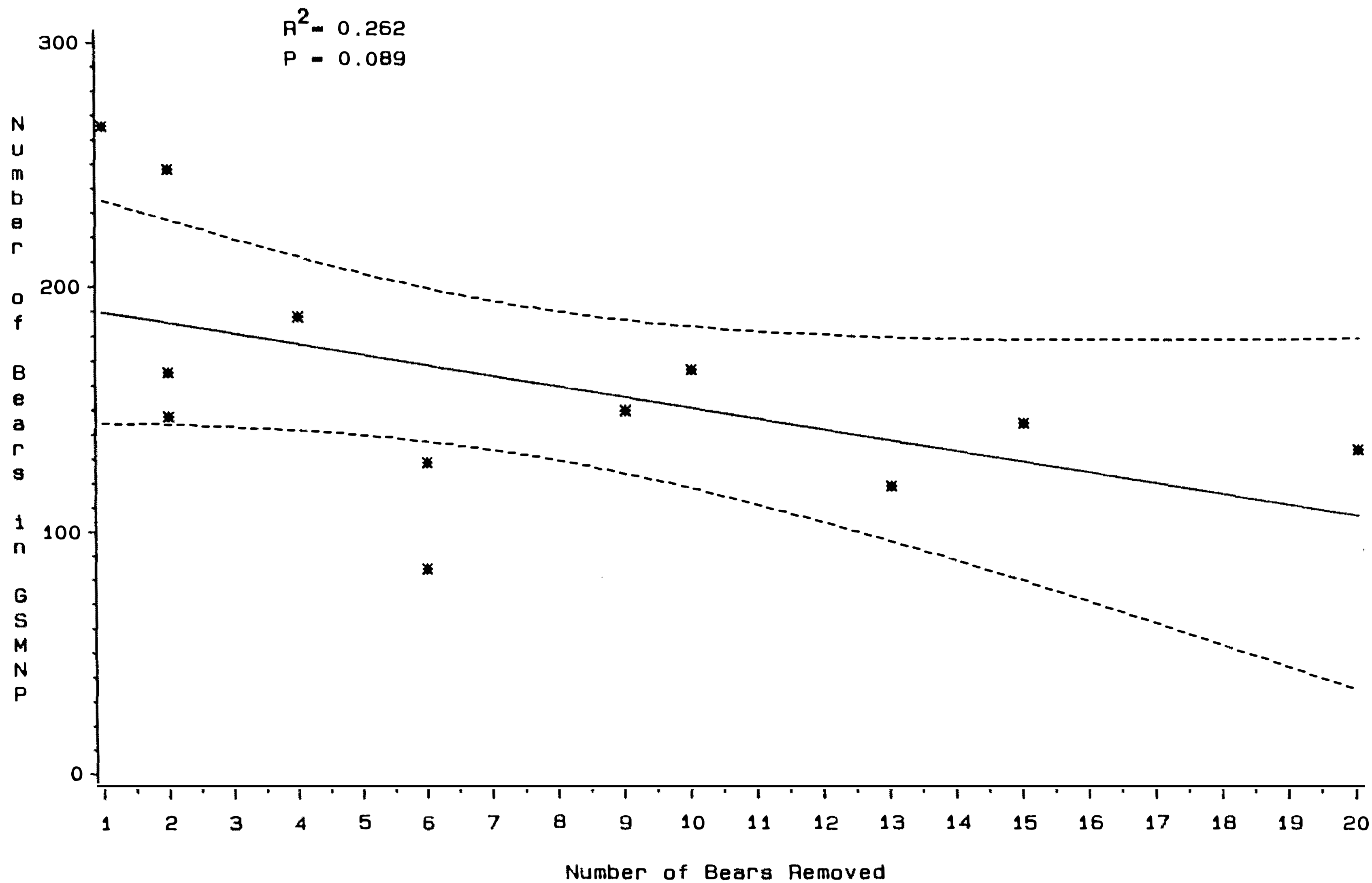


Tennessee (TWRA 1988) ($r = 0.611$, $\underline{P} = 0.016$) and was inversely, though insignificantly, related to Park management actions (e.g. removal from the Park) ($r^2 = 0.262$, $\underline{P} = 0.089$, Fig. 1.10). An increase in bears harvested corresponded to an increase in density (Fig. 1.11); an increase in removals of park bears was followed by a decrease in density.

Growth rate. The estimated intrinsic rate of growth, r, was 0.023 (2%) in GSMNP and 0.111 (11%) in the national forests combined.

Population model. The model simulations clearly demonstrated that within 20 years, hard mast availability can have a dramatic impact on bear numbers (Figs. 1.12 and 1.13). The numbers of female bears expanded in consecutive years of good mast; successive years of bad mast caused a substantial decline in bear numbers. Year-to-year variation in food supply also produced a decline in bear numbers. The trends in the numbers of NF bears were similar to those projected for Park bears (Fig. 1.13).

Fig. 1.10. Regression of the number of black bears in Great Smoky Mountains National Park on the number of bears removed from the Park, 1973-1987 ($Y = 194.079 - 4.393x$).



R^2 = 0.262
P = 0.089
Number of Bears in GSMNP
300
200
100
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Number of Bears Removed

Fig. 1.11. Annual fluctuations in the number of black bears in Great Smoky Mountains National Park and the number of bears harvested in Tennessee, 1973-1987.

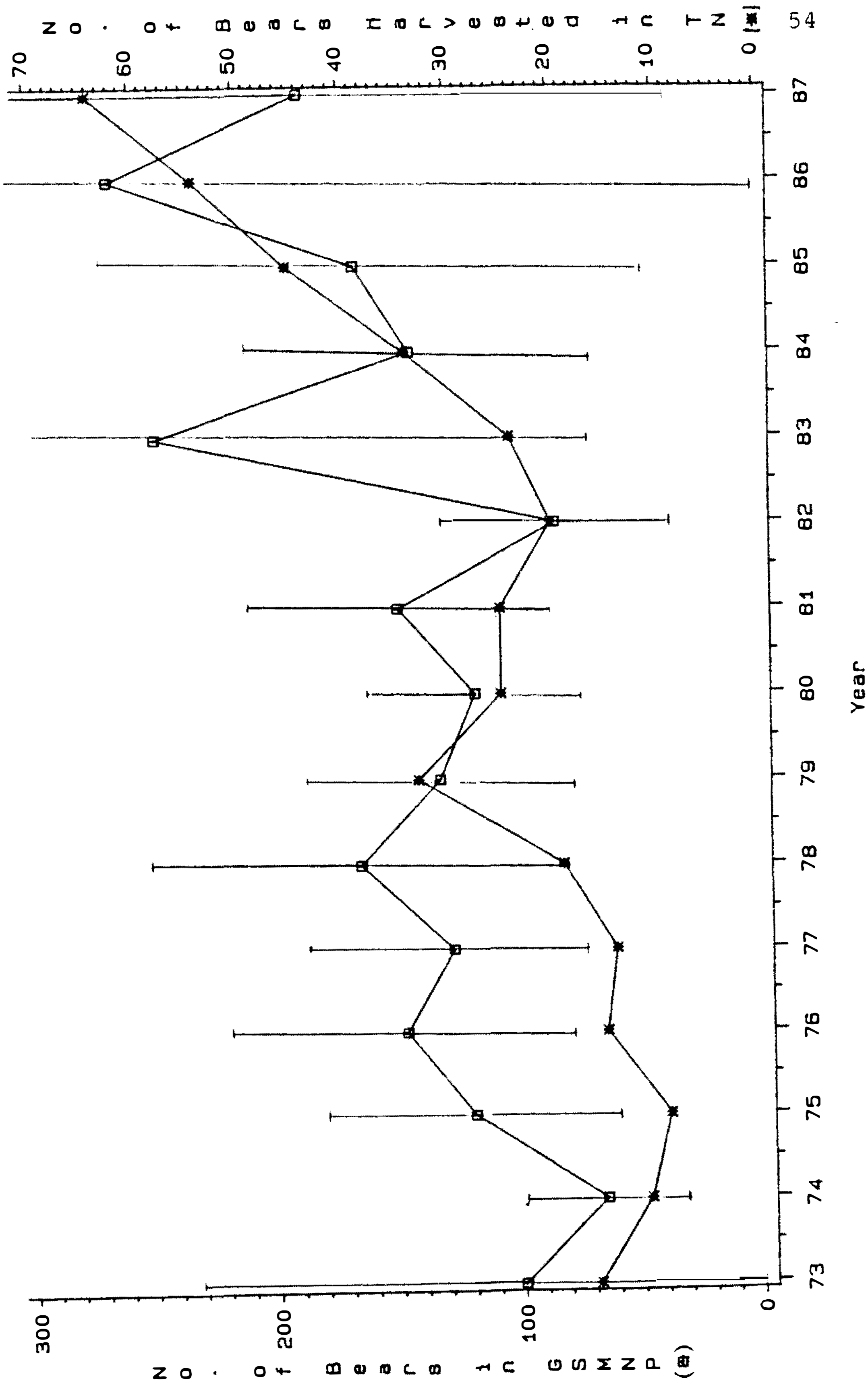
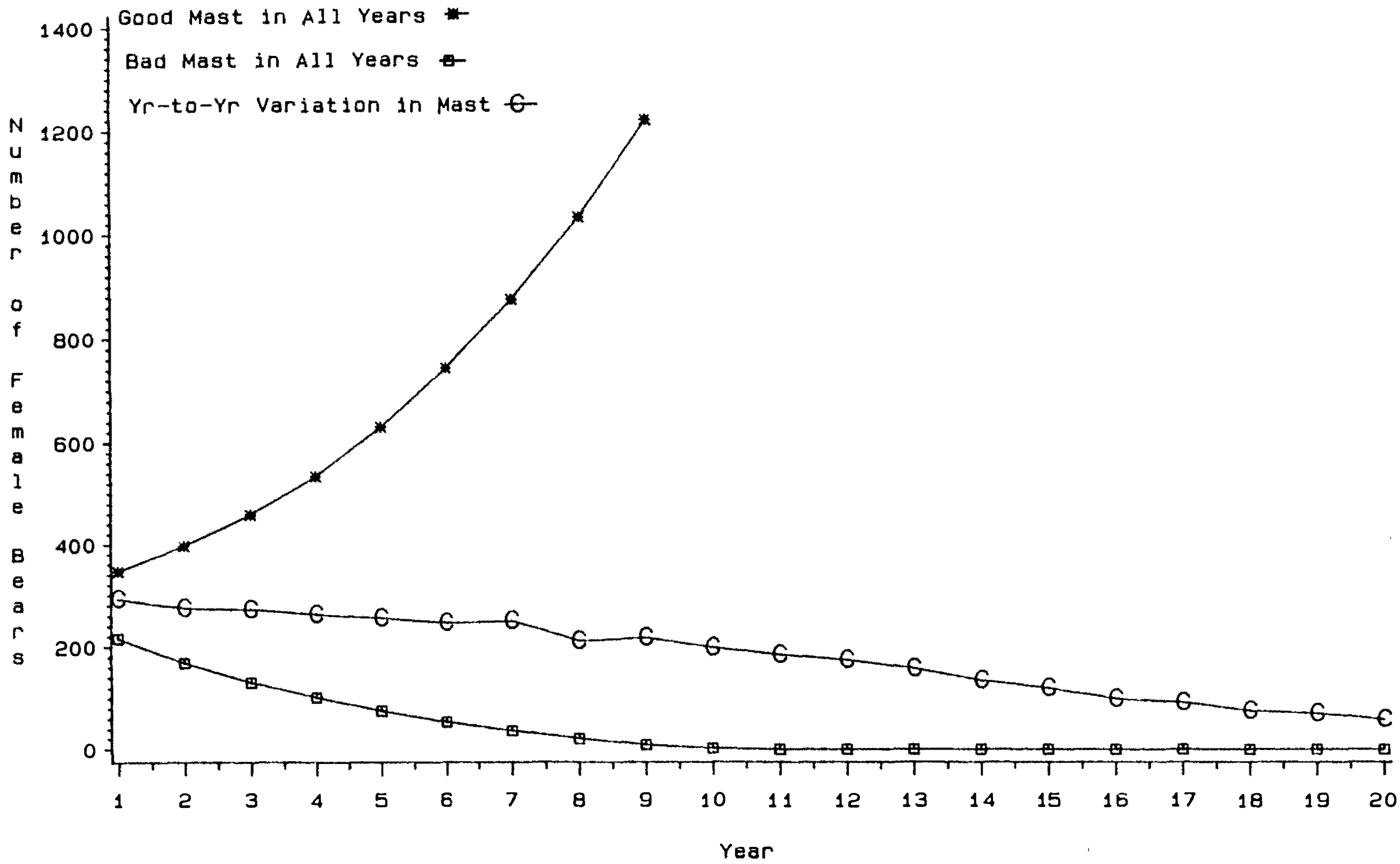
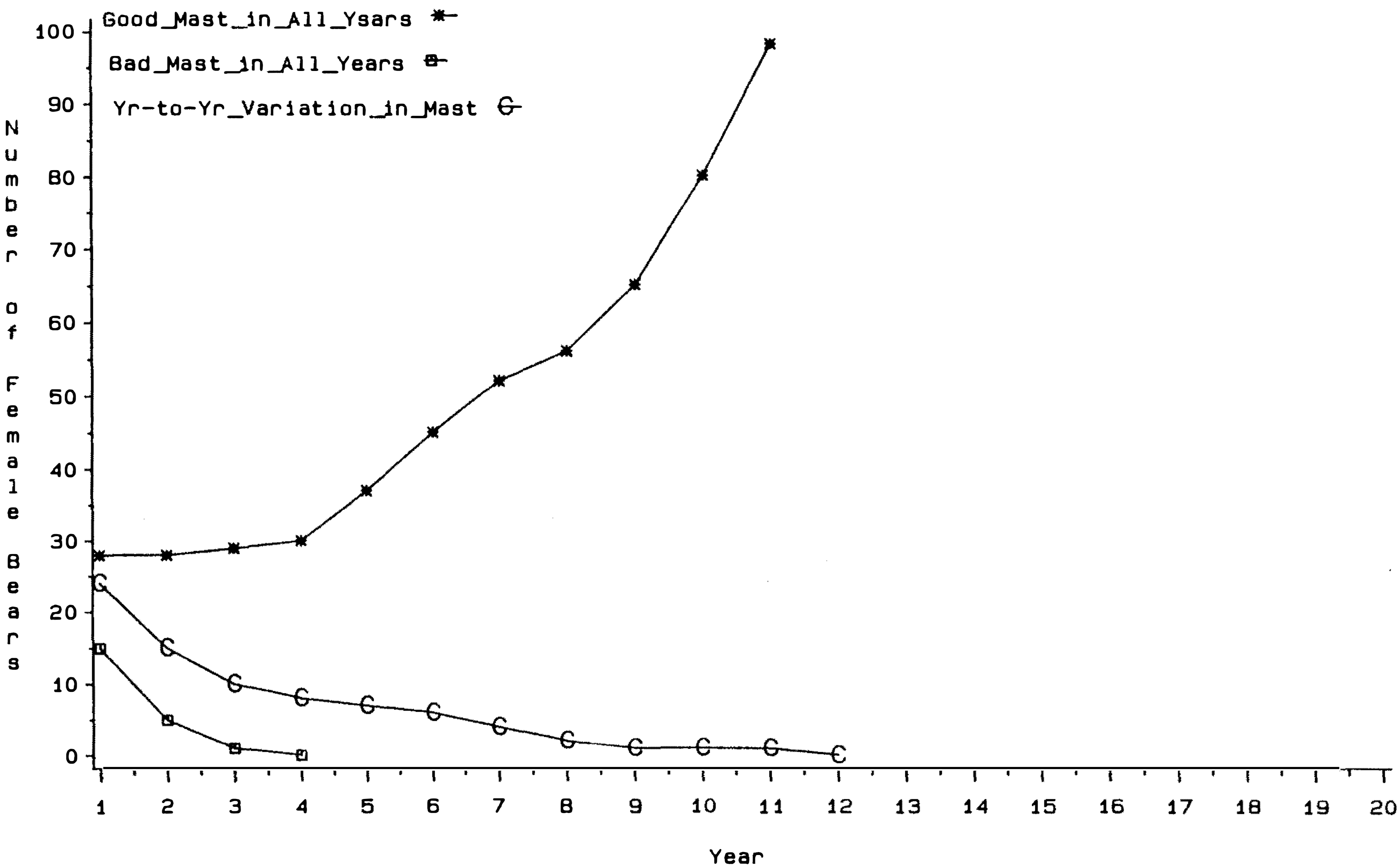

No. of Bears Harvested in TN (*)
70
60
50
40
30
20
10
0
No. of Bears in GSMNP (□)
300
200
100
0
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
Year

Fig. 1.12. Changes in the number of female black bears (based on model simulations) in Great Smoky Mountains National Park given an initial number of 297 females and varying mast availability.



Good Mast in All Years
Bad Mast in All Years
Yr-to-Yr Variation in Mast
Number of Female Bears
1400
1200
1000
800
600
400
200
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
Year

Fig. 1.13. Changes in the number of female black bears (based on model simulations) in Cherokee and Pisgah National Forests given an initial number of 20 females and varying mast availability.


Good_Mast_in_All_Ysars
Bad_Mast_in_All_Years
Yr-to-Yr_Variation_in_Mast
Number of Female Bears
0
10
20
30
40
50
60
70
80
90
100
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Year

DISCUSSION

Sex and Age Structure

The predominance of males in the capture sample can be explained by behavioral traits of males that increase their capture vulnerability (Johnson and Pelton 1980*b*). Male black bears typically have large home ranges (Garshelis and Pelton 1981, Rogers 1987) and, for a variety of possible reasons including aggression (Pelton 1982), food shortage (Rogers 1987), and avoidance of inbreeding (Packer 1979, Greenwood 1980, Rogers 1987), disperse farther than females; this dispersal and movement likely improves a male bear's chance of encountering a trap. The inexperience and movements of subadult males, who typically are in search of areas of few dominant males and plentiful food, improve their chance for capture. Other black bear studies reported a similar preponderance of males in their capture samples (Bunnell and Tait 1980, LeCount 1982, Carlock et al. 1983, Smith 1985, Rogers 1987, Hellgren 1988, Garshelis et al. 1989).

The age structure of bears in the Smokies suggests a slightly exploited population, and the significant decline in mean age of males suggests this exploitation is increasing. Hellgren (1988) defined exploited bear populations as those usually marked by mean ages <4 yr and that are <55% adult as found in North Carolina (Collins

1973) and other parts of the southern Appalachians (Carlock et al. 1983); unexploited bear populations generally are those with mean ages >6 yr and >60% adults as found in Arizona (LeCount 1982) and Arkansas (Smith 1985). Although possibly biased by the dispersal of young bears out of the Park, the age structure of bears in the Park (mean = 4.36 yr, 76% adult) suggests that Park bears are exploited less than bears in CNF (mean = 3.74 yr, 62% adult) and PNF (mean = 3.86 yr, 57% adult); that these mean ages are decreasing (Table 1.3) over time suggests that exploitation is increasing. Although the NF sanctuaries provide protection, they are comparatively small, have large boundary to interior ratios, and, consequently, do not provide the protection against poaching as found in the core areas of the Park. Park management may be partly responsible for the decline in mean age of male bears; nuisance males are the most often removed by Park officials (Beeman and Pelton 1980), and the removal of mature males would lower the average age of this segment of the population.

Male bears in the Smokies are, on average, younger than females. Aggression (Pelton 1982) in males and their large home ranges, portions of which often lie outside the protective boundaries of the Park (Beeman 1975, Garshelis and Pelton 1981) or sanctuaries, likely increase their vulnerability to harvest (legal/illegal); harvested animal populations are characterized by their young age structures (Downing 1980).

Reproduction

Except for black bear populations in Pennsylvania, the estrus period of the Smokies bear population was longer than reported elsewhere (see Rogers 1987, Alt 1990). Typically, estrus dates run from late June to late July; however, in areas of mild climate and abundant late summer and fall foods, the estrus period may last longer (Rogers 1987, Eiler et al. 1989). Plentiful food may explain the long estrus period (117 days) of the bear population in Pennsylvania. The fact that females in the Smokies, in particular young females, were in estrus later may reflect their nutritional condition (Jonkel and Cowan 1971, Eiler et al. 1989). Subadult females generally were in poorer condition than adult females (pers. observ.), weighed significantly less than mature females (Eiler 1981), and their estrus period may have been delayed by poor hard mast the previous fall and/or a late berry crop (Eiler et al. 1989).

With a few exceptions, the reproductive values of bears in this study were consistent with previous studies of black bears in the southern Appalachians (Collins 1973, Carlock et al. 1983, Eiler et al. 1989). Eiler et al. (1989) calculated a higher mean age at primiparity (4.6 yr) and a lower mean birth interval (2.2 yr) for bears of SM, however, these differences likely were insignificant. They (Eiler et al. 1989) also figured a higher mean litter size (2.6 cubs/litter). The fact that minimum estimates of counts of cubs in the dens were used may, in part, explain the disparity; also, this study's sample ($\underline{n}$ = 114) was larger and likely more representative. In a similar study area, Carlock et al. (1983) determined a mean litter size (1.9 cubs/litter) comparable to this study's. Eiler et al. (1989) figured an overall lactation rate (33%) identical to the one in this study; they, too, found that lactation rates increase with age of the female.

In comparison to other black bear studies in North America (Table 1.9), the mean reproductive values of SM bears are about mid-range; differences in these values among bear populations are food-related. In Montana, where huckleberry crops periodically fail, bears have the highest mean age at first reproduction (7.8 yr), the greatest mean birth interval (3.1 yr), and the smallest mean litter size (1.7) (Jonkel and Cowan 1971). In Pennsylvania, where food is consistently abundant, black bears have the highest reproductive rates of any wild bears (Kordek and Lindzey 1980, Alt 1982, 1990); the mean litter size (2.9) is the largest recorded for any wild bear population.

Food availability and habitat quality likely explain the differences in reproductive values of bears within the

Table 1.9. Major demographic features of selected black bear populations in North America.

Location and reference	Mean age at primiparity[a]	Mean birth interval[a]	Mean litter size	Adult mortality rate	Density (bears/km²)
Smoky Mts. This study	4.2	2.4	2.0	0.27	0.21-0.35
GSMNP This study	4.8	2.4	2.0	0.20	0.29
CNF+PNF This study	3.6	2.2	2.2	0.36	0.21-0.35
N.C. Collins, 1973	4.2[b]	2.0	1.8[b]	-	-
Shenandoah Natl. Pk., Va. Carney, 1985	3.9[c]	2.3	2.0	0.41M 0.08F	0.67-1.04
Great Dismal Swamp, Va. Hellgren, 1988	4.0[d]	-	2.1	0.42M 0.16F	0.46
Ont. Yodkis and Kolenosky, 1986 Kolenosky, 1989	6.0	2.0	2.4	0.17	0.2-0.6
White River Nat. Wildl. Refuge, Ark. Smith, 1985	-	2.4	2.3	0.05	0.17-0.42
Minn. Rogers, 1987	6.3	2.3	2.4	0.27M[b] 0.19F[b]	0.22
Mont. Jonkel and Cowan, 1971	7.8	3.1	1.7	0.14	0.23-0.48
Ariz. LeCount, 1982	-	-	1.9	0.02	0.33

Table 1.9. Continued.

Location and reference	Mean age at primiparity[a]	Mean birth interval[a]	Mean litter size	Adult mortality rate	Density (bears/km²)
Wash. Lindzey and Meslow, 1977	-	-	-	0.33M 0.21F	1.12-1.49
Alas. McIlroy, 1972	-	-	-	0.12	3.12

[a]Reported in years.

[b]Calculated by Bunnell and Tait 1981, 1985 from data provided in Collins, 1973.

[c]Calculated from data provided in Carney, 1985.

[d]Calculated from data provided in Hellgren, 1988.

Smoky Mountains. Hard mast is the principal food for black bears in the Smokies (Beeman and Pelton 1980, Eagle and Pelton 1983). In the national forests (CNF and PNF), where the percentage of lactating females and reproductive rates are greater and the mean age at primiparity and birth interval are lower than that of Park bears, oaks dominate the canopy (Beringer 1986, Seibert 1989). In the Park, oak canopy coverage is judged to be less than 40% (K. Langdon, Natl. Park Serv., pers. commun.). Also, the Park's mean index for mast (13.89 ± 9.056, n = 10 yr) is significantly (P = 0.0007) less than that of the national forests (31.71 ± 12.209, n = 15 yr).

Mortality

The recorded mortalities of marked bears provide only a sample of the different causes of death. The long period of study probably explains the preponderance of Park bears in the sample. The incentive of rewards for tag returns encourages the reporting of legal kills and likely explains their predominance in the sample. One might reasonably expect legal kills to be adults thus explaining their predominance. Poaching is considered a principal source of mortality in the study areas, but most illegal kills go unreported. There is little reason to suspect that poaching is more pronounced in the Park than the national forests (see Table 1.7).

By age group and sex, mortality rates of bears in the Smokies were largely comparable to those of other studies (Table 1.9). In an earlier study of bears of GSMNP, Beeman (1975) determined an overall mortality rate of 22%. Based on the survival of radio-collared bears, Seibert (1989) and others (Brody 1984, Beringer 1986) calculated an overall mortality rate of at least 35% for bears in PNF.

The low mortality among subadults in the Smokies (23%) is difficult to explain. High mortality among subadults is expected because of their vulnerability to harvest. Bunnell and Tait (1985) calculated a mortality rate for subadult black bears in Minnesota (34%) which was considerably higher than that figured for SM subadults. The subadult mortality rate generated from capture analysis (72%) likely was overestimated due to trapping bias; loss of marks also may bias the results (Alt et al. 1985).

The difference in the mortality rates of national forest (CNF and PNF) and Park bears is related to different management strategies. Hunting is prohibited in the Park but is permitted in all but relatively small portions of the national forest. Previous studies of PNF bears suggested the high mortality rates of subadults and adults, especially males, is due to intense hunting pressure, long hunting seasons, and high road densities which improve access by hunters (Brody 1984, Beringer 1986, Seibert 1989). High cub mortality in the Park may be due to differences in habitat quality between the Park and the national forests.

<u>Population Size and Stability</u>

Estimates of population density in the Smokies were consistent with previous estimates. Using various methods, Carlock et al. (1983) estimated the density of bears in SM at 0.18-0.46 bears/km^2 and in GSMNP at 0.08-0.59 bears/km^2. Using radioisotopes and scat counts, Pelton and Marcum (1975) placed the GSMNP density at 0.251 bears/km^2. Based on capture data, Brody and Stone (1987) estimated the density of bears in PNF to be 0.193 bears/km^2. In comparison to other populations in North America, these estimates are low to intermediate on a low-high density continuum (Table 1.9).

Although the Jolly-Seber method of population estimation violates the fewest assumptions and incorporates the most data (Carlock et al. 1983, Hallett et al. 1991), the population estimates, especially those of the national forest, must be interpreted carefully. Generally, mark-recapture analyses require large samples. In the Park, trapping was extensive, and a large number of bears usually were caught each year (mean: 41.3 ± 12.16 bears/yr, $\underline{n}$ = 17 yr); however, sampling in the national forests was less extensive, and far fewer bears were captured yearly (9.4 ± 6.23 bears/yr, $\underline{n}$ = 20 yr). Also, the ratio of trapline length to area was much greater in the national forests (16 km:97km^2 = 0.16) than in the Park (40km:506km^2 = 0.08); although well-distributed, the comparatively fewer traplines in the Park left some areas unsampled. Adjusting for this disparity by randomly disregarding one half ($0.08 \div 0.16 = 0.5$) of the trap records of NF bears generated perhaps more realistic population estimates of 15 bears (0.18 bears/km^2) and 10 bears (0.09 bears/km^2) in CNF and PNF study areas, respectively.

Few estimates of the intrinsic rate of population growth (r) of black bears exist. For bears in Shenandoah National Park and Great Dismal Swamp, VA, $r = 0.000$ (Carney 1985), and $r = 0.0032$ (Hellgren 1988), respectively, providing evidence that these bear populations are virtually stable. Estimates for SM indicate a slightly (2%, GSMNP) to moderately (11%, NF) increasing population. These estimates, too, need to be interpreted cautiously as slight variations of the life history values (see Appendix B) used for calculating r can cause variations in its estimation.

The density and growth rates of the SM bear population are consistent with the findings of Tanner (1966). For most animal populations, Tanner (1966) argues that density is correlated inversely with growth. In the national forests, where bear density is low, the growth rate is high; in the Park, where the density is relatively high, the growth rate is low. This inverse relationship tends to promote stability among animal populations (Tanner 1966); unless subjected to large-scale habitat alterations, naturally-occurring populations rarely grow to excessive numbers or decline to extinction (Tanner 1966).

In illustrating the importance of hard mast to reproduction and survival of black bears in the Smokies, the model simulations indicate both outcomes: exponential growth and extinction. Despite the extreme outcomes, the model is useful in that it does illustrate the importance of food and consequent trends in population growth.

However, the fact that the model predicts a population decline even with year-to-year variation in mast indicates weaknesses in the model. Mast availability described as good, bad, and average may be inadequate in portraying oak mast production in the Smokies; more qualitative divisions (e.g. fair, fairly good/poor, etc.) might be more consistent with reality and improve the model's predictive capabilities. Although adding a variable (e.g. food availability) to the model adds realism, the Leslie matrix is a simple model. It inherently predicts extremes in population growth or decline depending on the initial numbers in the population (S. Stringham, pers. commun.). The low initial numbers of NF bears (e.g. 20 females, see Fig. 1.13) probably explain their rapid decline in bad mast years and failure to respond in good ones. Given possible periodic fluctuations in mast production and the long-lived nature of black bears, 20 years is not enough time to adequately assess the variations of mast and its influence on bear reproduction; undoubtedly, more years of data would improve the validity of the model.

The model also fails to include other factors which influence the population. Soft mast, such as berries (*Rubus* spp., *Vaccinium* spp., *Gaylussacia* spp.), cherries (*Prunus serotina*) and grapes (*Vitis* spp.), likely moderates the effects of hard mast failures (Garshelis and Pelton 1981, Eiler et al. 1989). Individual variation in bears also is neglected in the model as are the direct effects of immigration and density. In the future, revisions of the model should attempt to incorporate some of these effects.

Population Control and Management

Extrinsic and intrinsic factors control the bear population of the Smoky Mountains. Habitat quality (e.g. hard mast), apparently, is limiting the population, but other factors also appear important in regulating the numbers of black bear in these mountains.

The data clearly indicated that hard mast production and reproduction are closely linked. Specifically, hard mast availability is important to female reproduction and cub survival. These data and those from another study in the same area (Eiler et al. 1989) indicated an increase in the percentage of lactating females in years following abundant mast, particularly white oak mast; years of poor mast yield (e.g. 1982) resulted in decreased cub survival. Mast appears to be an important population regulator in both the national forests and the Park. These findings support those of others (Jonkel and Cowan 1971, Rogers 1976, 1987, Herrero 1978, Bunnell and Tait 1981, LeCount 1982, Beecham 1983, Elowe 1987, Eiler et al. 1989) who argue that nutrition is the chief control of bear reproduction.

Some authors (Mech 1970, Free and McCaffrey 1972, Craighead et al. 1974, McCullough 1981, Shaffer 1983, Stringham 1983) propose that reproduction in mammals may be density-dependent; however, this is not conclusively supported by data on black bears in the Smokies. Conceivably, mortality due to hunting may, in part, cause the elevated reproductive rates of females in the national forests where harvest rates are high; if hunting can reduce the density enough so that fewer bears enjoy more habitat, then reproductive rates of the fewer females would improve. In Minnesota, Mech (1970) showed that the twinning rates of the Isle Royale moose herd was higher after wolves arrived on the island and preyed on moose. Mech (1970) suggested that the high productivity in the moose herd was a result of improved availability of habitat due to the limiting influence of wolves. Although correlation analysis indicates an inverse relationship between density and the lactation rates of CNF (r = -0.053), PNF (r = -0.249), and GSMNP bears (r = -0.135), this relationship is not significant ($\underline{P} \geq 0.686$). A compensatory response may exist, but its effects likely are overshadowed by those of nutrition.

However, legal and illegal hunting is common and may influence the SM population of bears, especially in the national forests. Man is a chief cause of mortality in the national forests, particularly in Pisgah National Forest where hunting pressure is intense (Brody 1984, Beringer 1986, Seibert 1989). Nearly 90% of recorded mortalities in the national forests and nearly 75% of recorded mortalities in the Park were attributed to the legal or illegal harvest (see Table 1.7). Although data are lacking, there is much anecdotal evidence to suggest that poaching is a significant source of mortality in portions of the Park (e.g. Parson's Branch Road).

Black bear abundance in GSMNP also appears to be determined by density-dependent mortality. Increases in the Park's density are positively correlated with Tennessee's legal harvest and negatively, though not significantly, correlated with the yearly percentage of subadults (r = -0.188, $\underline{P} = 0.502$). With increasing density, young bears in GSMNP may be forced to the Park's less-protected perimeter, where they are subjected to more hunting and poaching. Earlier studies of bears in the Park (Beeman 1975, Garshelis and Pelton 1981) indicate that social intolerance, which is prevalent between adult and subadult males particularly during poor mast years, causes bears to disperse to the Park's perimeter and beyond.

The reports of the killing of snared bears, usually subadults, by adult males (Jonkel and Cowan 1971, Kemp 1976) prompted the hypothesis of adult males as population regulators (Ruff 1982). Others (Bunnell and Tait 1981, McCullough 1981, Young and Ruff 1982, Lindzey et al. 1983, Rogers 1987), since, have argued the importance of male-male interactions and subsequent dispersal in regulating bear populations. Interactions appeared to increase with density (Stokes 1970), and decrease with food abundance (Egbert and Stokes 1976, Garshelis and Pelton 1981). Beecham (1980 in Ruff 1982) and LeCount (1982) argued that subadult dispersal is the most important regulator of unexploited populations; however, in an exploited population of bears in Montana, Jonkel and Cowan (1971) implicated male antagonism (e.g. agonistic encounters, cannibalism) as the primary intrinsic force in regulating that black bear population. Regulation by agonistic encounters has been noted in other animal populations such as red deer (*Cervus elaphus*) (Wynne-Edwards 1962), voles (*Microtus* spp.) (Christian 1963), and muskrats (*Ondatra* spp.) (Errington 1963).

In the Park, management also may influence the size of the bear population. Removal of large numbers of problem bears, usually mature males, in certain years (e.g. 20 bears removed in 1979, W. J. Cook, Natl. Park Serv., unpubl. data) combined with the periodic egress of males in search of food appear to decrease population numbers. These findings are contrary to those of Kemp (1976) who noted that the removal of adult bears from a population in northern Alberta caused an influx of subadults and an increase in population size. However, the effects of the removal of bears from the Park explains only 26% of the variation in density and likely are overshadowed by the effects of nutrition and subadult dispersal.

Disease and parasites probably have very little impact on the health of the SM bear population. In 3 years of handling over 100 bears, only 1 death was attributed to disease (toxoplasmosis). Cook (1982) examined nearly 300 bears in GSMNP for presence of disease and parasites and concluded that Park bears were healthy. In some studies (see Rogers 1983, 1987), diseases in bears, particularly of the gums and teeth, have been noted, but no decimation of bear populations by disease or parasites has been reported (Pelton 1982, Rogers 1987).

In sum, several ingredients are important in sustaining a viable black bear population in the Smoky

Mountains: 1) Food, particularly hard mast, is vital to black bear reproduction. Forestry practices and land management promoting the production of hard mast also would foster black bear production. 2) The protection of adult females whose fertility increases with age and weight. The establishment of bear sanctuaries and late hunting seasons is important in protecting the female segment of this population and others (Rieffenberger 1976, Raybourne 1978). 3) The continuation of study of black bears in the Smokies. Long-term studies of large animals, such as this study, are few (Shaffer 1983); data collection, especially on reproduction, is difficult but is essential to understanding the population dynamics of long-lived animals such as black bears. Although the demographic data suggest a population in fair to good health, these data need surveillance to ensure a stable age structure, prevent overexploitation, and guard against limits to population viability such as environmental uncertainty (e.g. unpredictable changes in weather or food supply) and natural catastrophes (e.g. fires or drought) (Shaffer 1987). 4) The curtailment of poaching and monitoring of the legal harvest both of which may have a significant impact on the population. Hunting pressure may be increasing due to the commercialization of body parts, but public education would lower the loss of bears to poaching and management actions (e.g. the removal of panhandler bears from the Park). Although currently no serious detrimental effects of harvest to the bear population can be detected, harvest combined with habitat loss to fragmentation (Harris 1984, Maehr 1984), road and resort development, the gypsy moth (*Lymantria dispar*) which can defoliate and kill mast producers, and improper timber practices may increase the bear's vulnerability to hunting, decrease reproduction, and, as a consequence, jeopardize the last sizeable population of black bears in the southeast.

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PART II

SOME DEMOGRAPHIC COMPARISONS OF WILD AND PANHANDLER BEARS IN THE SMOKY MOUNTAINS

INTRODUCTION

Black bears (Ursus americanus) in southeastern North America have lost approximately 90% of their original range (Pelton 1986). Many bear populations that remain in the southeast exist in contiguous areas of natural forest. These areas are largely public lands: state and national forests and parks, national wildlife refuges, and state game lands. The forests of the Smoky Mountains (SM) and neighboring ranges, conserved largely by Great Smoky Mountains National Park (Park or GSMNP) and Cherokee, Nantahala, Chattahochee, and Pisgah National Forests, harbor a significant number of black bears, some of which come into direct and frequent contact with humans.

Because of a variety of factors, including the violation of National Park Service regulations regarding food and bears (Pelton 1975, Singer and Bratton 1980), visitor density (Singer and Bratton 1980, Keay and Van Wagtendonk 1983), bear density, and habitat condition (Harms 1979), panhandler (problem bear) activity in the Smokies is common. Park officials, in recent years, report an average of 158 incidents/year (SD = 76.7, n = 11) of personal property damage, a large part of which is caused by problem black bears (W. J. Cook, Natl. Park Serv., unpubl. data).

Panhandlers in the Smokies have been characterized in previous studies (Beeman and Pelton 1976, 1980; Eiler 1981; Tate 1983; Tate and Pelton 1983). Here and elsewhere, many researchers have indicated that black bears utilizing high-energy, human-made food grow faster and mature earlier (Rausch 1961, Rogers 1976, Rogers et al. 1976, Alt 1980, Eiler 1981, Tate 1983, Tate and Pelton 1983, Rogers 1987). Differences in characteristics between these bears and black bears that survive on natural foods only (wild bears) likely reflect habitat quality.

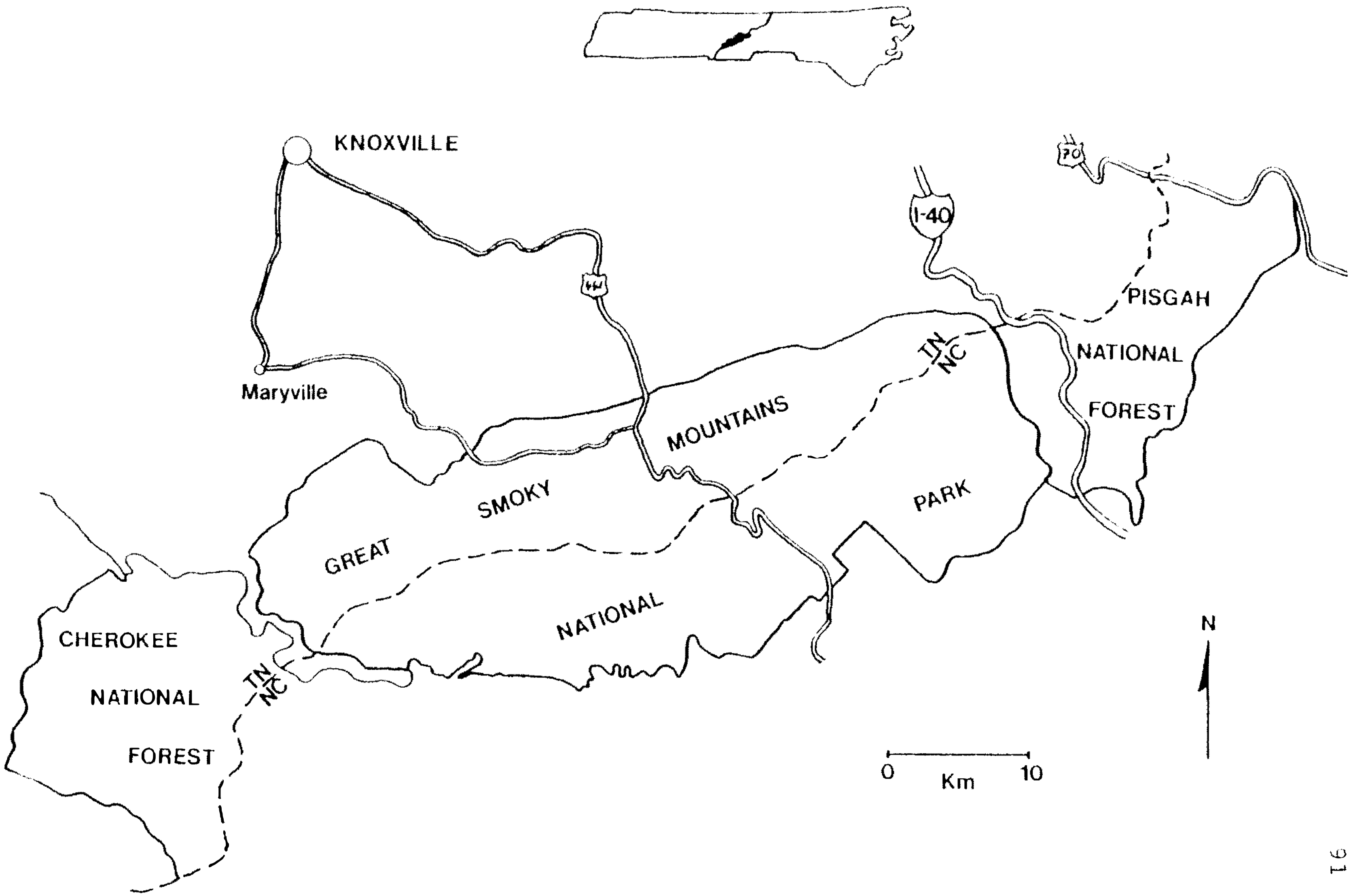
In this paper, the demographic characteristics of a relatively large sample of wild and panhandler bears were compared and related to the nutritional qualities of habitat in the Smoky Mountains.

STUDY AREA

Data were collected in the northwest quarter of Great Smoky Mountains National Park (Fig. 2.1) from 1968-1989. The Park consists of 2074 km^2 divided nearly equally between Tennessee and North Carolina and is visited by nearly 10 million people annually. The Park is characterized by steep ridges, narrow valleys, coves, and fast-flowing streams (King and Stupka 1950). Elevation ranges from 230 to 2035 m (Pelton et al. 1980). Average annual temperatures vary from 14°C at low elevations to 8°C on upper slopes (Shanks 1954). Considered a temperate rain forest (Thornthwaite 1948), the Park receives 140 cm of annual precipitation at low elevations and 230 cm at high elevations (Stephens 1969). Six major forest types are recognized (Shanks 1954): cove hardwood, hemlock (*Tsuga canadensis*), northern hardwood, open oak-pine (*Quercus* spp.-*Pinus* spp.), closed oak, and spruce-fir (*Picea rubens*-*Abies fraseri*). Understory vegetation is dominated by mountain laurel (*Kalmia latifolia*), rhododendron (*Rhododendron* spp.), blueberries (*Vaccinium* spp.) and huckleberries (*Gaylussacia* spp.).

The Pisgah National Forest (PNF) study area comprises 114 km^2 (Beringer 1986) in North Carolina (Fig. 2.1). This area, northeast of GSMNP, is similar to the Park in terms of climate and geology. Elevations commonly range from

Fig. 2.1. Location of Great Smoky Mountains National Park and Cherokee and Pisgah National Forests in eastern Tennessee (TN) and western North Carolina (NC).


KNOXVILLE
Maryville
I-40
70
PISGAH
NATIONAL
FOREST
GREAT
SMOKY
MOUNTAINS
NATIONAL
PARK
TN
NC
TN
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CHEROKEE
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439 to 1411 m (Beringer 1986). Of the nearly 2000 plant species identified in this national forest, several are predominant in the overstory including white (*Quercus alba*), northern red (*Quercus rubra*), scarlet (*Quercus coccinea*) and chestnut oaks (*Quercus prinus*), hickory (*Carya* spp.) and yellow-poplar (*Liriodendron tulipifera*); nearly 90% of the study area is in hardwoods with oak or oak-associates comprising 74% (USFS 1981 in Beringer). In 1971 the area was designated as the Harmon Den Bear Sanctuary with hunting restricted to that of small game (excluding raccoon) and deer (Beringer 1986). Bear poaching within and around the sanctuary likely is a significant source of mortality. Logging operations, managed by the U. S. Forest Service, continue today although not with the same intensity as in the early 1900's (Beringer 1986). The University of Tennessee has conducted black bear research in Pisgah National Forest since 1982.

In the same mountain range, but to the southwest of the Park, lies the Cherokee National Forest (CNF) study area (Fig. 2.1). It is situated within the Tellico Ranger District, Tennessee, and constitutes about 760 km^2 (Clevenger 1986). It also is similar in geology and climate to that of the Park. Elevations range from 450 to 1550 m, and the area is generally characterized by steep mountains and fast-flowing streams (Clevenger 1986). It is 99% forested with 5 major plant communities recognized:

cove hardwood, northern hardwood, oak-hickory, pine, and mesic hemlock (Clevenger 1986). The forest cover was significantly altered by logging and associated fires until the Forest Service purchased the land in the 1930's (Clevenger 1986). A 124-km^2 segment of the study area serves as a bear refuge reserved for small game hunting (Clevenger 1986). Black bear data were collected in the Cherokee study area from 1972-1984.

MATERIALS AND METHODS

Wild and panhandler bears were captured from spring through fall, 1968-1988, with snares or culvert traps. Trapping and marking techniques described by Johnson and Pelton (1980a,b) were used. In most cases, a 20:10:2 mg/ml mixture of rompun, ketaset, and carbocaine was used to sedate the bears, though, in the early years of the study, other immobilizing drugs were employed (Cook 1982). A premolar extracted from each bear was sectioned and stained (Eagle and Pelton 1978) for age determination (Willey 1974). Bears whose ages were >3 yr were considered adults. Females were examined for evidence of lactation, and to aid in its detection, oxytocin or pitocin was administered. Body weights were measured with spring scales (300- and 500-lb capacity); these weights were later converted to kilograms. In addition to the body measurements outlined in LeCount (1986), the following were measured: head width at the zygomatic arch; head length - from the tip of the nose to the apex of the sagittal crest; forearm circumference - at the point immediately distal to the elbow.

Litter size was determined from visual observations at capture and during winter den investigations. Sonagram analysis also was used to assess litter size (Wathen 1983).

Field data were organized and statistically analyzed with the statistical analysis systems (SAS Institute 1985). Because within-year recaptures were low (<5% for wild and <15% for panhandler bears) and to incorporate all the data, recaptures were used in the analysis unless otherwise indicated; analyses incorporating data just on individual bears were similar in terms of significant results (McLean unpubl. data; see Table 2.1). Mast index values (C. J. Whitehead, oak mast yields on wildlife management areas in Tennessee, Tenn. Game and Fish, unpubl. rep., 11pp., 1969; see Appendix A) were generated from mast data collected annually (Tennessee Wildlife Resources Agency, unpubl. data). Age of primiparity, based on evidence of lactation and/or young was determined from reproductive histories. Chi square served to assess the degree of association between 2 or more variables. The t-test served to compare means of the body measurements and ages. Based on mean weights for wild and panhandler bears, the analysis of covariance was used to model the growth rates of bears.

Black bears of the Smokies likely belong to one population although some of the analysis may suggest otherwise. Emigration and immigration of bears among the study areas (Quigley 1982, Carr 1983) indicate a single population; long-distance movements, particularly by males, ensure gene flow between bears in the national forests and the Park and between wild and panhandler bears. However, because management in the Park differs from that in the national forests, one might expect regional differences within the population; demographic features of Park bears might vary from those of the national forest. A portion of this analysis attempts to examine some of the possible differences.

RESULTS

Data from 1210[a] (604 individual) wild and 492[a] (274 individual) panhandler black bear captures were examined. Most (83%, n = 1413) of the bears were handled in Great Smoky Mountains National Park.

Sex and Age

The status (wild or panhandler) of the bear and its gender were associated (X^2 = 3.7, 1 df, P = 0.056). Of the wild bear captures, 54% (n = 557) were males, whereas 60% (n = 289) of the panhandler captures were males.

Status also was significantly (P < 0.001) associated with maturity (subadult or adult). Of the male captures, 29% (n = 152) of the wild and 47% (n = 101) of the panhandler bears were subadults (X^2 = 22.9, 1 df). Of the female captures, 19% (n = 86) of the wild and 37% (n = 54) of the panhandler bears were subadults (X^2 = 17.9, 1 df).

The mean ages[b] of wild (4.4 ± 2.64 [SD] yr, n = 559) and panhandler (3.2 ± 2.93 yr, n = 194) black bears were significantly different (P ≤ 0.004). Wild males had an average age of 3.9 ± 2.09 yr (n = 323), and the mean age of

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[a]These numbers represent totals; sample size for each analysis will vary based on data available.

[b]Mean ages based on individual captures.

panhandler males was 2.9 ± 2.40 yr (n = 115). Wild females averaged 4.9 ± 3.16 yrs (n = 236), and panhandlers 3.7 ± 3.52 yrs (n = 79). Maximum ages were 15.5 yr for wild males, 12.5 yr for panhandler males, 22.5 yr for wild females, and 16.5 yr for panhandler females.

Body Size

Adult panhandlers were significantly heavier and longer and had larger necks, chests, and heights at the shoulder than their wild counterparts (Table 2.1). Subadults were significantly heavier than wild bears (Table 2.2).

Wild bears of the national forests were bigger than Park bears (Table 2.3). Adults in Cherokee and Pisgah National Forests were significantly heavier (Table 2.3). Subadults were significantly heavier, and males were significantly larger in all body measurements (Table 2.4).

Panhandlers grew faster than their wild counterparts (Fig. 2.2). Panhandler males grew the fastest; wild females the slowest. The growth of females leveled off, whereas males continued to grow; wild females reached their greatest weight (25 kg) at age 9, and panhandler females appeared to attain their maximum weight (35 kg) at age 12. Contrasts performed with the analysis of covariance revealed that growth of panhandlers was significantly (P < 0.05) different from their wild counterparts for all ages above age 2. Autocorrelation did not confound this

Table 2.1. Mean values of body measurements of adult wild and panhandler black bears handled in the Smoky Mountains, 1968-1988.

	Wild bears[a]		Panhandler bears	
Body measurement	Male	Female	Male	Female
Weight	73.8[b] (29.3, 335)[c]	50.1 (13.6, 352)	102.3* (40.9, 101)	60.3* (14.0, 84)
Total length	156.5 (17.9, 311)	142.7 (14.0, 339)	167.2* (17.9, 82)	152.7* (11.2, 79)
Neck	55.0 (10.2, 309)	45.5 (5.8, 335)	58.4* (11.0, 74)	47.5* (5.7, 79)
Chest	86.1 (14.3, 308)	75.2 (9.4, 336)	93.6* (18.9, 73)	79.3* (11.0, 79)
Shoulder	81.0 (11.0, 309)	73.0 (7.1, 340)	85.4* (9.1, 72)	76.6* (6.3, 77)
Forearm	32.7 (5.2, 308)	28.1 (3.2, 335)	33.7 (5.2, 75)	29.7* (5.9, 79)
Head width	27.5 (4.8, 239)	24.8 (3.8, 273)	28.2 (4.8, 57)	26.3* (2.4, 73)
Head length	33.4 (3.6, 312)	30.7 (1.9, 341)	34.3* (3.5, 83)	30.4 (2.7, 80)

[a] Includes 1 or 2 individuals not classified as Park or national forest bears.

[b] By individual: weight of wild males = 67.3 ± 26.64 kg (n = 201) and panhandler males = 91.8 ± 42.40 kg (n = 42), P = 0.0001.

[c] (SD, n)

* Denotes significant ($P < 0.05$) difference from the wild counterpart.

Table 2.2. Mean values of body measurements of subadult wild and panhandler black bears handled in the Smoky Mountains, 1968-1988.

	Wild bears[a]		Panhandler bears	
Body measurement	Male	Female	Male	Female
Weight	36.4 (21.5, 165)[b]	27.7 (14.6, 107)	57.6* (47.9, 147)	35.5* (24.1, 98)
Total length	125.4 (23.0, 148)	117.1 (20.4, 97)	126.9 (30.0, 115)	119.4 (29.8, 85)
Neck	40.0 (9.4, 145)	36.0 (8.2, 99)	40.5 (12.2, 113)	36.6 (9.7, 83)
Chest	65.4 (15.1, 146)	60.2 (14.9, 96)	67.1 (20.0, 114)	60.9 (18.4, 84)
Shoulder	63.8 (12.9, 146)	58.9 (12.3, 93)	62.7 (14.6, 104)	61.2 (15.5, 81)
Forearm	25.7 (5.7, 145)	22.9 (4.8, 95)	25.7 (6.3, 110)	22.6 (5.5, 83)
Head width	21.8 (4.5, 126)	19.5 (4.3, 80)	22.6 (4.3, 95)	21.4* (4.3, 79)
Head length	28.5 (4.1, 147)	26.7 (3.5, 96)	27.7 (5.0, 115)	25.6 (4.9, 84)

[a] Includes 1 or 2 individuals not classified as Park or national forest bears.

[b] (SD, _n_)

* Denotes a significant (_P_ < 0.05) difference from the wild counterpart.

Table 2.3. Mean values of body measurements of adult wild black bears handled in Great Smoky Mountains National Park (GSMNP) and Cherokee (CNF) and Pisgah (PNF) National Forests, 1972-1988.

	GSMNP		CNF and PNF	
Body measurement	Male	Female	Male	Female
Weight	71.6 (26.2, 275)ª	48.5 (11.7, 279)	84.0* (39.3, 60)	55.4* (16.5, 72)
Total length	156.1 (16.8, 261)	142.7 (10.2, 278)	158.5 (22.8, 50)	142.6 (24.8, 61)
Neck	54.6 (9.7, 264)	44.8 (4.8, 276)	57.3 (12.4, 45)	48.6* (8.5, 59)
Chest	86.4 (14.0, 262)	74.9 (9.3, 278)	85.0 (15.9, 46)	76.9 (10.1, 58)
Shoulder	81.5 (10.5, 259)	73.5 (6.4, 279)	78.6 (12.9, 50)	70.8 (9.5, 61)
Forearm	32.8 (5.0, 264)	27.9 (2.5, 277)	32.0 (6.1, 44)	29.1 (5.3, 58)
Head width	27.8 (4.5, 206)	24.7 (2.9, 227)	25.9 (6.1, 33)	25.5 (6.6, 46)
Head length	33.2 (3.4, 262)	30.5 (1.6, 280)	34.3 (4.5, 50)	31.3* (2.9, 61)

ª (SD, n)

* Denotes a significant ($P < 0.05$) difference from the GSMNP counterpart.

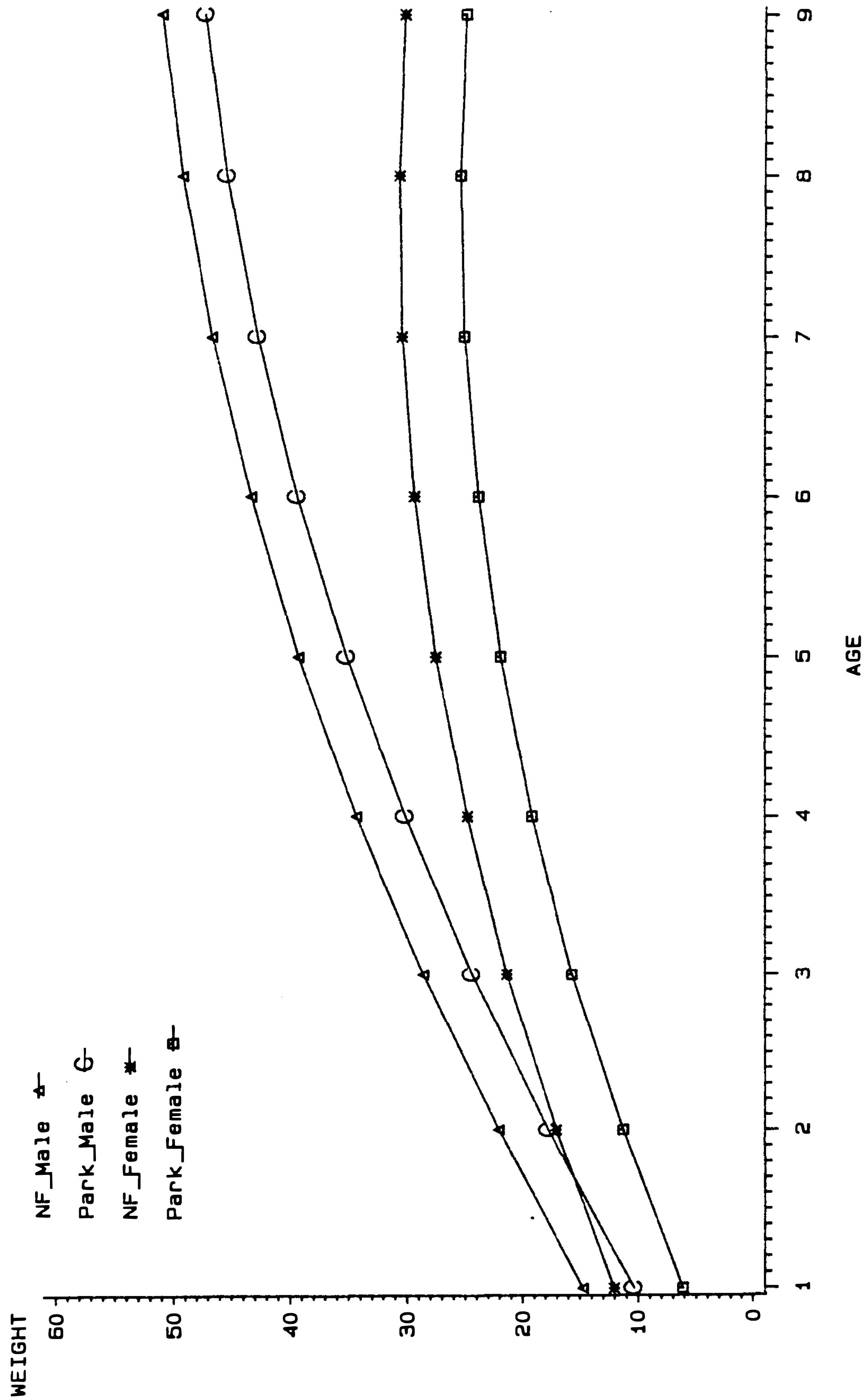
Table 2.4. Mean values of body measurements of subadult wild black bears handled in Great Smoky Mountains National Park (GSMNP) and Cherokee (CNF) and Pisgah National Forests (PNF), 1972-1988.

	GSMNP		CNF and PNF	
Body measurement	Male	Female	Male	Female
Weight	32.4 (20.9, 115)[a]	26.1 (15.6, 66)	44.7* (20.3, 49)	29.8 (12.6, 40)
Total length	120.8 (22.8, 106)	116.2 (22.5, 61)	137.0* (19.4, 42)	118.7 (16.5, 36)
Neck	37.8 (8.1, 105)	34.4 (8.6, 63)	46.0* (10.2, 40)	38.7* (6.7, 36)
Chest	61.8 (13.4, 105)	57.6 (15.1, 60)	73.7* (14.9, 40)	64.6* (13.7, 36)
Shoulder	63.2 (12.3, 105)	58.9 (11.5, 57)	65.5* (14.4, 41)	58.9 (13.7, 36)
Forearm	24.5 (5.1, 105)	22.3 (4.5, 59)	28.4* (5.8, 39)	24.0 (5.2, 36)
Head width	21.1 (3.9, 93)	20.4 (3.8, 52)	23.8* (5.5, 33)	17.9* (4.7, 28)
Head length	27.5 (3.7, 105)	26.2 (3.5, 60)	31.1* (3.9, 42)	27.6 (3.4, 36)

[a] (SD, *n*)

* Denotes a significant (*P* < 0.05) difference from the GSMNP counterpart.

Fig. 2.2. Growth curves of male and female, wild and panhandler black bears in the Smoky Mountains, 1968-1988.



WEIGHT
0
10
20
30
40
50
60
AGE
1
2
3
4
5
6
7
8
9
NF_Male
Park_Male
NF_Female
Park_Female

analysis (Durbin-Watson D = 2.24, $P > 0.05$).

Fertility

Panhandler females were more fertile than wild bears. The number of lactating females was significantly associated with status ($X^2 = 12.026$, 1 df, $P \leq 0.001$). Fifty-six percent ($n = 34$) of the panhandlers were lactating, whereas only 33% ($n = 146$) of the wild females were. In addition, 19% ($n = 17$) of the panhandler and only 2% ($n = 5$) of the wild females were observed with litters of 3 or 4 young. The mean minimum age of primiparity was 3.5 yr ($\pm$ 0.71, $n = 2$) for panhandler and 4.2 yr ($\pm$ 1.04, $n = 21$) for wild bears.

Fertility varied by study area. Fifty percent ($n = 41$) of the adult bears in the national forests and only 29% ($n = 105$) of the Park females were lactating ($X^2 = 13.228$, 1 df, $P = 0.001$). Moreover, the mean minimum age of primiparity for females in the national forests (3.60 $\pm$ 0.699 yr, $n = 10$) was significantly ($P = 0.004$) less than that for Park females (4.82 $\pm$ 0.982 yr, $n = 11$).

DISCUSSION

Sex and Age

Males predominated among panhandler bears; this is consistent with most studies of problem bears. In an earlier study of homing of bears in the Smokies (Beeman and Pelton 1976), 87% of the relocated bears were males. Other studies indicated a similar preponderance of males among problem bears (Erickson et al. 1964, Harger 1967, Wasem 1968, Sauer et al. 1969, Beeman 1975, Piekielek and Burton 1975, Payne 1978, Beeman and Pelton 1980, Singer and Bratton 1980, McArthur 1981, Tate and Pelton 1983).

Male predominance may be explained by the transient nature of males and the greater likelihood that males rather than females with cubs would be relocated (Tate and Pelton 1983). Males have larger home ranges (see Rogers 1987: 19) and, for a variety of possible reasons including aggression (Pelton 1982, Tate and Pelton 1983), food shortage (Rogers 1987), and avoidance of inbreeding (Packer 1979, Greenwood 1980, Rogers 1987), they disperse farther than females (Rogers 1987).

Lower survival among panhandlers likely contributes to their low mean age. Females are more vulnerable to poaching and death from collisions with automobiles due to their proximity to roadsides. Beeman and Pelton (1976) suggested that a low mean age among males resulted from the removal of adult males by Park officials. Males are vulnerable to legal harvest and poaching mainly due to their large home ranges (Pelton 1982), portions of which often lie near or outside the protective boundaries of the Park. Jonkel and Cowan (1971) and Rogers (1987) indicated that subadult males disperse farther than females; these males, in search of areas of few dominant males and plentiful food, are likely to encounter a panhandling opportunity and become more vulnerable, particularly in concentrations of human activity and foods (Rogers 1987).

Body Size

Panhandlers were not only bigger than wild black bears but grew faster; two other studies comparing panhandler and wild bears in the Park had similar findings. Tate (1983) found that male (n = 45) and female (n = 17) panhandlers weighed significantly ($P < 0.02$) more than their wild counterparts of the same age. Using growth curve models based on Brody (1964), Eiler (1981) compared the weights of 54 male and 25 female panhandlers with 174 wild males and 158 wild females and found that panhandlers weighed more than their wild counterparts of the same age.

Such differences in size and growth reflect the panhandlers access to and consumption of high-energy, human-made foods. These foods supplement the bear's natural diet and are high in sugars and other carbohydrates that are readily converted to and stored as fats (Tate 1983). Rausch (1961) reported that well-fed, captive black bears developed more rapidly than wild ones. Rogers (1976) also reported that captive bears raised on rich diets developed more rapidly than bears on natural ones. In Michigan, subadult bears feeding at dumps made superior weight gains over bears that fed exclusively on natural foods (Rogers et al. 1976, Rogers 1987). Bears in Pennsylvania, reputedly the fastest growing of any wild black bears (Rogers 1987), attain greater weights because of relatively abundant and consistent natural foods and sources of food (garbage, corn fields, bird feeders, apiaries) deliberately or inadvertently furnished by humans (Alt 1980).

Fertility

Problem bears were more productive than wild black bears. In the same study area, Tate (1983) revealed that litters of 3 or 4 cubs among panhandlers were common and that some panhandler females mated at 2.5 yr. Although this study's sample of primiparous females was small (n = 2), panhandler females first had young at age 3.5, and a high percentage of all female panhandlers were observed with litters of 3 or 4 young.

Improved fertility is common among panhandler bears or bears that supplement their natural diets with high-energy, human-made food. Rogers (1976) reported that both sexes of captive bears fed on rich diets reached maturity at 2.5 yr. He also found that black bears that supplement their diets with garbage tend to have litters at a younger age (Rogers 1987). Female bears in Michigan frequenting sources of garbage had significantly larger litters than females that did not visit such sources (Rogers et al. 1976). In Pennsylvania, where black bears commonly exploit garbage dumps and corn fields, the average litter size is 2.9 (Alt 1982); 38% of the 2-year old females taken in the fall harvest were pregnant and the first litter of females averaged 2.39 cubs and subsequent litters averaged 3.23 cubs (Kordek and Lindzey 1980). These natality rates are the highest of any reported for wild black bears (Rogers 1983).

Habitat Quality

Differences in demographic characteristics of wild and panhandler bears likely reflect habitat quality. The larger size and faster growth rates of panhandlers in the Smokies corroborate the contribution of high-energy human-made foods, and suggest the failure of natural foods to provide adequate nutrition. Wild black bears in the Smokies rely on oak mast which is often cyclic in production (Zahner 1991). Wathen (1983) and Eiler et al. (1989) indicated that reproductive success of black bears follows years of abundant white oak mast. Beecham (1980) suggested that females in poorer habitat grew more slowly than females in areas replete with food. Over 90% of the females studied in Massachusetts produced young following years of good oak mast; only 29% produced young following years of bad mast production (Elowe 1987). The high growth and fertility rates of black bears in Pennsylvania, where food is consistently abundant, differ dramatically from those in bears in the Smokies; rough estimation indicates that even the largest and fastest-growing black bear in the Smokies (male panhandler) grows to a maximum weight that is about 30% less than that of the average-sized male in Pennsylvania.

Differences in size of wild bears within the Smoky Mountains probably were due to differences in fall mast production. Mast distribution in these mountains is patchy, and previous studies suggested a greater and more even distribution of fall mast in the national forests than in the Park (Brody 1984, Eiler et al. 1989). A comparison of mean mast index values, representing at least 10 years, for the Park (2.45 ± 0.66, $\underline{n} = 10$) and Cherokee National Forest (3.29 ± 1.18, $\underline{n} = 15$) indicates that mast production in the national forest is significantly greater ($\underline{P} = 0.033$). In Pisgah National Forest, the percent of the canopy in oak, estimated at 60-80% (Beringer 1986), is considerably greater than the 30-40% (K. Langdon, Natl.

Park Serv., pers. commun.) estimated for the Park.

Habitat quality also may dictate the amount of panhandler activity. In the Park, panhandlers constitute only 5-10% of the bear population (Beeman and Pelton 1980), and they eat predominantly natural foods (Beeman and Pelton 1980, Tate 1983). Increases in the production of these foods would not only boost the carrying capacity of the local habitat, but, conceivably, decrease the amount of panhandler activity. In Yosemite National Park, problem black bears are large (Guse 1970) and comprise 50-80% of the total population (J. A. Keay, Natl. Park Serv., pers. commun.). They may depend on artificial foods which constitute at least 15% of their diets (Graber and White 1983); this and problem bear abundance may indicate that the Yosemite bear population has exceeded the carrying capacity of the natural habitat.

Differences in demographic characteristics between wild and panhandler bears also may reflect the effects of human-made food, the availability of which varies with panhandler bear management. The relatively few, but highly-visible, panhandlers in the Park, which consumed relatively small amounts of food over a short period of time, were not intensively managed until about 1976. Through public education, sanitization of campgrounds and trash cans, relocation of problem bears, and other management, the incidence of panhandling in the Park decreased; by the late

1970's and early 1980's, panhandlers became less of a problem than a decade earlier. In comparing the demographic characteristics of panhandler and wild bears for the 2 periods, before 1976 and after 1980, significant differences were detected. The differences in weight, and neck and chest circumferences between wild and panhandler bears handled before 1976 were significantly ($\underline{P} \leq 0.002$) greater than those differences between wild and panhandler bears captured after 1980. For example, prior to 1976, the mean weights of male adult panhandler and wild bears were 135.0 ± 42.1 kg ($\underline{n} = 26$) and 71.8 ± 23.4 kg ($\underline{n} = 56$), respectively; these weights were significantly different ($\underline{P} < 0.0001$). However, there was no significant difference in the mean weights of adult males that were handled after 1979 ($\underline{P} = 0.15$); the average weight of panhandlers was 80.8 ± 23.9 kg ($\underline{n} = 44$) and that of the wild bears' was 73.3 ± 32.1 kg ($\underline{n} = 169$). Apparently, then, the panhandlers' access to and consumption of human-made food before 1976 made appreciable differences in terms of their size.

In conclusion, the analysis indicates significant differences in the demographic characteristics of wild and panhandler bears. These differences likely reflect the influence of high-energy, human-made foods, habitat quality, and the effects of bear management. Given these factors, forestry practices and land management should promote the production of natural foods, particularly hard mast. To ensure the protection of Park visitors and their property, unnatural foods must be kept from bears. Managers might expect increased panhandler activity especially given changes in habitat due to the unreliability of hard mast in the Smokies, the loss of the American chestnut (*Castanea dentata*) as a significant mast producer (Zahner 1991), and an impending gypsy moth (*Lymantria dispar*) infestation which could damage or destroy oaks (*Quercus* spp.) and other major mast producers.

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PART III

PREDICTING WEIGHT FROM BODY MEASUREMENTS OF BLACK BEARS IN THE SMOKY MOUNTAINS

INTRODUCTION

In studies of large animals, the estimation of weight from body measurements can facilitate the collection of weight data. Typically, body weight is measured with heavy, cumbersome spring scales, and their use is sometimes impractical in the field. Because weight and body measurements are highly correlated, Talbot and McCullough (1965) and others (McEwan and Wood 1966, Smart et al. 1973) found that body measurements can be used to predict weights of ungulates. In all species of North American bears, significant linear relationships between weight and body measurements have been reported (Cherry and Pelton 1976, Payne 1976, Stirling et al. 1977, Glenn 1980, Nagy et al. 1984, Swenson et al. 1987). However, Swensen et al. (1987) suggested that the accuracy of the predictive equations may vary with the location of the bear population. Here, a relatively large sample is used to develop equations which predict weight given several body measurements of black bears (*Ursus americanus*) in the Smoky Mountains (SM).

MATERIALS AND METHODS

Black bears were trapped in the spring, summer, and fall, 1968-1988, in the Smoky Mountains of Tennessee and North Carolina. The study areas included the northwest quarter of Great Smoky Mountains National Park, a 114-km^2 portion of Harmon Den in Pisgah National Forest, and a 124-km^2 section of the Tellico Ranger District in Cherokee National Forest.

Once captured, a 20:10:2 mg/ml mixture of ketamine, rompum, and carbocaine was used to sedate the bears, though, in the early years of the study, other immobilizing agents were employed (Cook 1982). Sex and status (wild or panhandler) of the bear were recorded. Bears were weighed with spring scales (300- and 500-lb capacity) to the nearest pound; these weights were later converted to kilograms. In addition to the body measurements as outlined in LeCount (1986), the following were measured: head width - from the crest of the zygomatic arch, across the forehead to the crest of the opposite arch; head length - from the tip of the nose to the apex of the saggital crest; ear length - from the inside base of the ear to its tip; forearm circumference - at the point immediately distal to the elbow.

All correlations, regressions, and transformations were performed with the Statistical Analysis Systems (SAS

Institute 1985). To avoid possible exaggeration in body size, no recaptures were used in this analysis. Because the relationship between weight and linear body measurements is curvilinear (expressed as $W = aX^b$, Nagy et al. 1984), natural logarithms were used to linearize the relationship giving the equation: $l_nW = a + B\ l_nX$.

RESULTS

Body measurements were collected from 604 wild and 274 panhandler black bears. Of the body measurements, total length ($r = 0.853$), and neck ($r = 0.900$) and chest ($r = 0.888$) circumferences were the most significantly ($\underline{P} \leq 0.0001$) correlated with weight. Weight was then regressed on these 3 measurements to produce predictive equations for SM bears (Table 3.1). All equations indicated strong linear relationships, but the relationships were strongest for panhandlers (Table 3.1). The predictive capabilities of these equations appeared reliable especially at the low-to-mid range of weights (Table 3.2). There was no positive serial correlation to confound these relationships (Durbin Watson $D \geq 1.587$, $\underline{P} \geq 0.01$).

Although the logarithmic transformations produced the strongest relationships, different linear relationships between weight and the other body measurements were examined. Logarithmic transformation of the values representing chest circumference and weight produced a weaker, yet significant linear relationship for wild ($r^2 = 0.846$, $\underline{P} \leq 0.0001$, $\underline{n} = 311$, CV = 6.249, Fig. 3.1) and panhandler ($r^2 = 0.876$, $\underline{P} \leq 0.0001$, $\underline{n} = 108$, CV = 8.585, Fig. 3.2) males. The combination of total length and chest girth squared also was a significant predictor of weight (all bears: $r^2 = 0.862$, $\underline{P} \leq 0.0001$, $\underline{n} = 749$, CV = 21.52).

Table 3.1. Predictive equations for weights (kg) of black bears in the Smoky Mountains, 1968-1988.

Status	Sex	Predictive equation	r^2 [a]	n	CV(%)
Wild	M	$\ln W$[b] $= -7.861 + 0.773 \ln C$[c] $+ 0.972 \ln N$[d] $+ 0.936 \ln T$[e]	0.932	308	4.16
Wild	F	$\ln W = -8.760 + 0.247 \ln C + 0.972 \ln N + 1.576 \ln T$	0.912	222	4.35
Wild	M+F	$\ln W = -8.136 + 0.432 \ln C + 1.067 \ln N + 1.216 \ln T$	0.925	530	4.31
Pan[f]	M	$\ln W = -10.152 + 0.425 \ln C + 0.980 \ln N + 1.710 \ln T$	0.942	106	5.93
Pan	F	$\ln W = -9.927 + 0.970 \ln C + 0.671 \ln N + 1.424 \ln T$	0.949	98	5.98
Pan	M+F	$\ln W = -10.009 + 0.634 \ln C + 0.910 \ln N + 1.551 \ln T$	0.946	204	5.94
Wild+ Pan	M	$\ln W = -8.518 + 0.734 \ln C + 0.925 \ln N + 1.143 \ln T$	0.933	418	4.82
Wild+ Pan	F	$\ln W = -9.480 + 0.358 \ln C + 0.948 \ln N + 1.647 \ln T$	0.940	326	5.02
Wild+ Pan	M+F	$\ln W = -8.960 + 0.524 \ln C + 0.961 \ln N + 1.387 \ln T$	0.937	744	4.95

[a]All regressions are significant ($P \leq 0.0001$).

[b]W = weight.

[c]C = chest measurement (cm).

[d]N = neck measurement (cm).

[e]T = Total length (cm).

[f]Panhandler.

Table 3.2. Weight estimates (kg) from predictive equations of wild bears captured in the Smoky Mountains, 1968-1988.

Chest girth (cm)	Males	Females
34	7.2 (6.7-7.6)[a]	6.9 (6.4-7.5)
36	7.0 (6.4-7.6)	7.0 (6.4-7.4)
40	8.6 (8.1-9.1)	9.7 (9.0-10.5)
44	14.5 (13.9-15.2)	9.1 (8.5-9.7)
46	11.6 (11.0-12.2)	14.8 (14.2-15.5)
51	17.1 (16.5-17.8)	18.7 (17.7-19.7)
53	14.6 (13.9-15.4)	18.5 (17.8-19.3)
55	21.0 (20.3-21.8)	26.4 (25.6-27.1)
60	27.7 (26.9-28.6)	30.6 (29.9-31.4)
64	38.2 (36.7-39.6)	37.6 (36.3-38.9)
69	36.1 (35.4-36.9)	32.9 (32.1-33.8)
74	41.9 (40.8-4.92)	45.3 (44.3-46.3)
80	54.5 (53.0-56.1)	50.3 (49.0-51.6)
83	64.8 (63.4-66.3)	45.1 (43.6-46.7)
85	57.9 (56.3-59.5)	47.8 (46.3-49.4)
89	72.1 (70.5-73.8)	65.8 (62.8-70.0)
96	62.9 (59.9-65.9)	71.2 (68.4-74.1)
100	108.1 (104.6-111.8)	-
114	127.2 (122.6-132.0)	-
125	123.0 (117.4-128.6)	-
134	124.1 (117.8-130.8)	-

[a]The range in parenthesis is the 95% confidence interval.

Fig. 3.1. Regression of weight (ln) on chest circumference (l_n) of wild male black bears in the Smoky Mountains ($\ln W = -6.432 + 2.382X$).

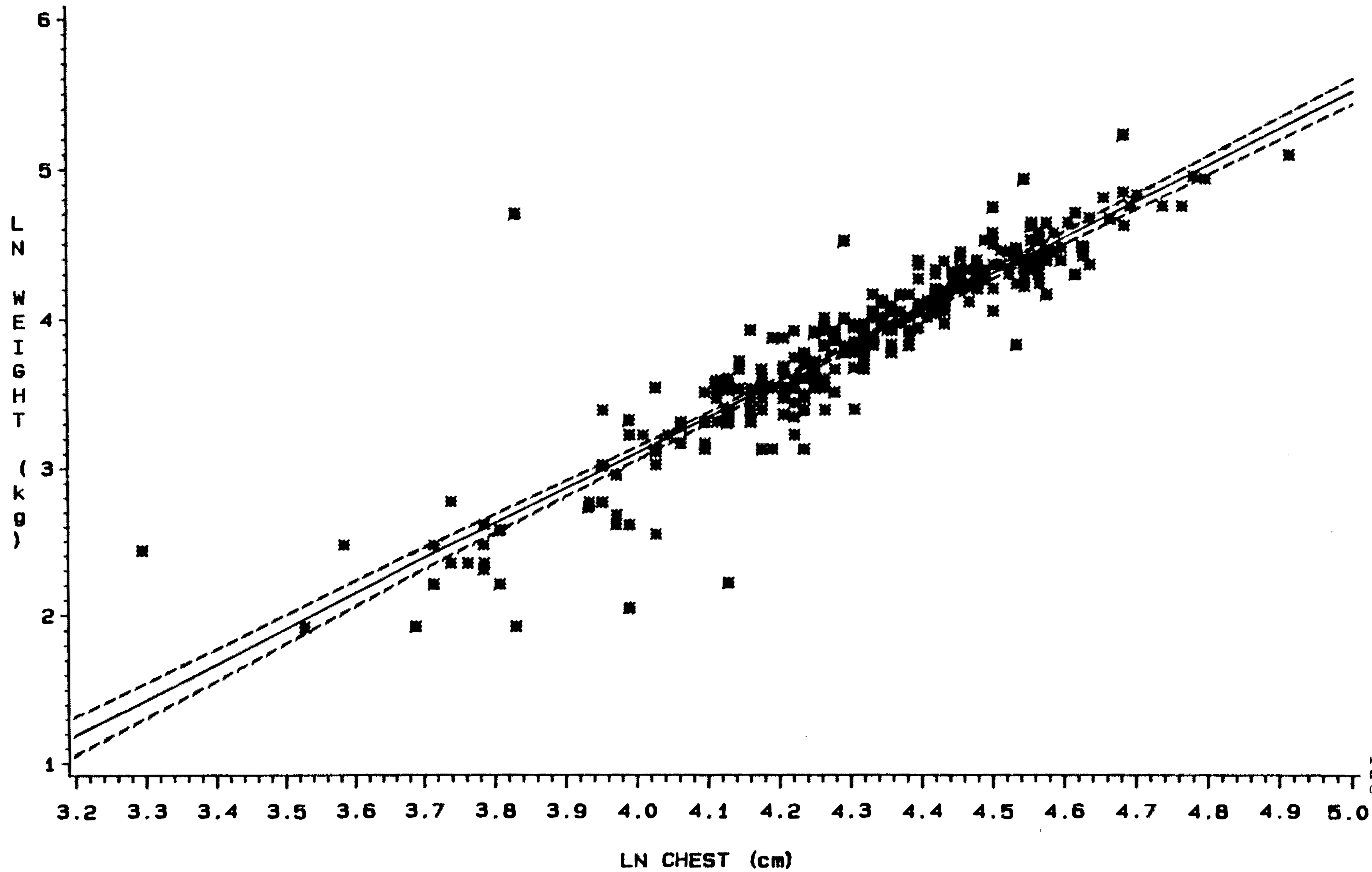
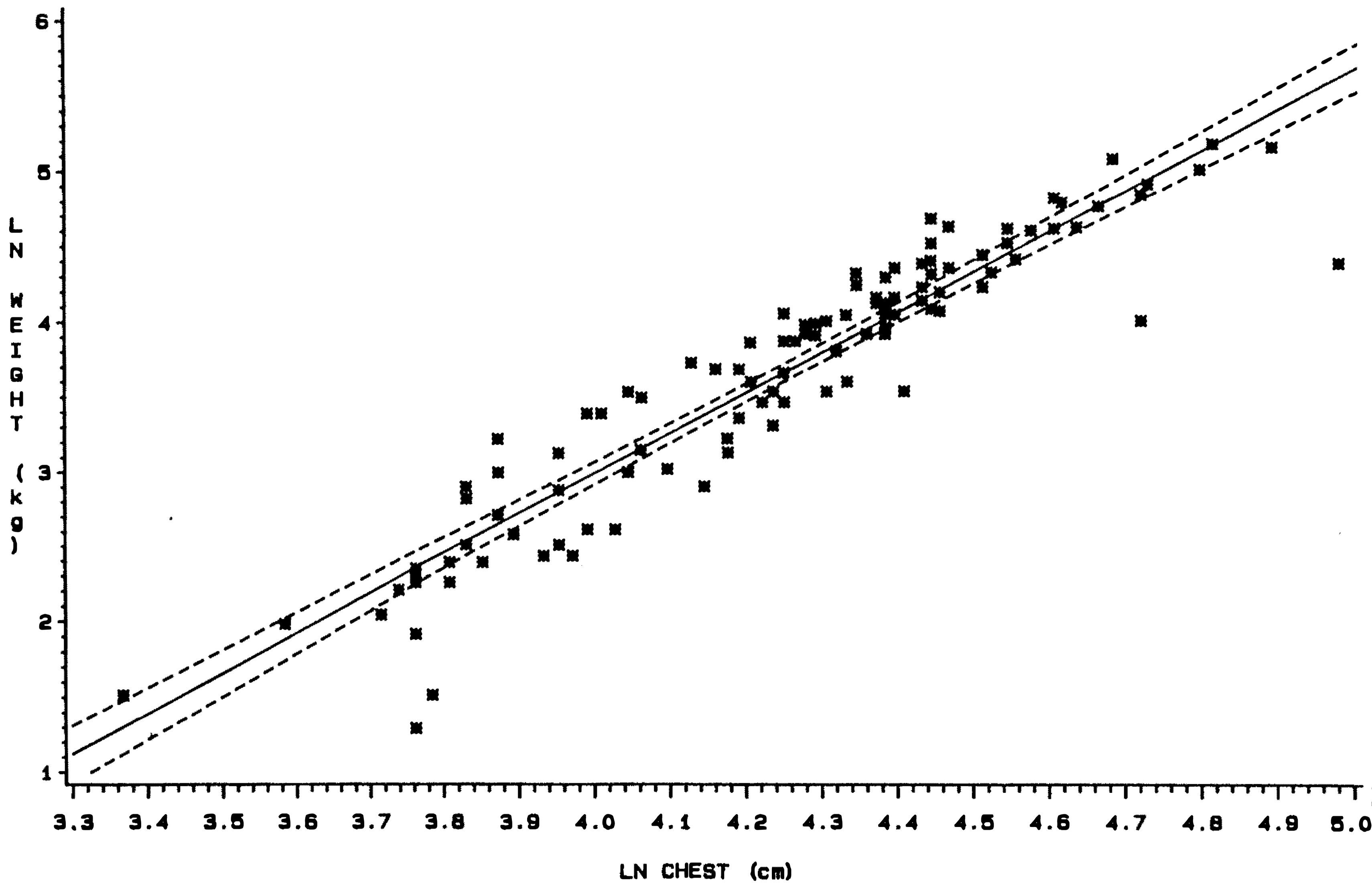

LN WEIGHT (kg)
LN CHEST (cm)
1
2
3
4
5
6
3.2
3.3
3.4
3.5
3.6
3.7
3.8
3.9
4.0
4.1
4.2
4.3
4.4
4.5
4.6
4.7
4.8
4.9
5.0

Fig. 3.2. Regression of weight (ln) on chest circumference (l_n) of panhandler male black bears in the Smoky Mountains ($\ln W = -7.679 + 2.667X$).


LN WEIGHT (kg)
6
5
4
3
2
1
3.3
3.4
3.5
3.6
3.7
3.8
3.9
4.0
4.1
4.2
4.3
4.4
4.5
4.6
4.7
4.8
4.9
5.0
LN CHEST (cm)

DISCUSSION

Using a large sample of black bears, chest, neck, and total length were the best predictors of body weight; these results are similar to those of another study in the same area (Cherry and Pelton 1976). Using a small sample (77 bears), Cherry and Pelton (1976) found chest and forearm circumferences, total length, and forefoot width to be the best predictors of body weight. The predictive capabilities of their equations dropped off markedly at the heavier weight range whereupon the weight could be better guessed than estimated (Cherry and Pelton 1976). The equations developed here appear to be more accurate than previous ones although reliability also declines at the heavier weights; some bias in converting the logarithmic values to the original units can be expected (Beauchamp and Olson 1973) and might explain some of this unreliability. Using these equations, bear researchers in the Smoky Mountains can forego guessing and the inconvenience of spring scales.

Using chest girth as the principal predictor for weight of black bears in North America, Swenson et al. (1987) concluded that the most accurate equations were those developed within geographical regions. Equations presented in this study best represent black bears in the Smoky Mountains; should these equations be applied elsewhere, accuracy likely would diminish.

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SUMMARY AND CONCLUSIONS

1. Under the direction of Dr. Michael Pelton and with a team of graduate students, over 20 years of data on sex, age, survival, and reproduction were collected from 1702 black bears trapped in the Smoky Mountains. These data were compiled and analyzed to determine the demographic and morphological characteristics of the bear population in the Smoky Mountains.

2. The predominance of males (mean = 55%, $\underline{n}$ = 569), particularly in the young (≤5 yr) age classes, likely was explained by the transient nature of males and inexperience of young males.

3. The mean age of captured bears was 4.36 yr. Mean age of female bears (4.96 yr) was significantly older than that of males (3.92 yr). The oldest male and female bear were 15.5 and 22.5 yr, respectively. Mean age of Park bears (4.52 yr) was significantly older than that Cherokee National Forest (3.74 yr) but not of Pisgah National Forest (3.86 yr). Also, the proportion of adults was greatest in the Park (76%) indicating less exploitation than in either of the national forests. Mean age for males captured during the first half of the study, 1972-1979, was significantly older than that of males captured after 1979, suggesting an increase in exploitation.

4. Female bears exhibited signs of estrus between 5

June and 19 September (106 days). The mean minimum reproductive age was 4.24 yr for SM, 4.82 yr for Park and 3.60 yr for national forest females. The mean birth interval was 2.35 yr for SM, 2.39 yr for Park, and 2.20 yr for NF bears. The mean litter size was 2.04 cubs for SM, 1.96 cubs for Park and 2.25 for NF bears. The reproductive rates and the percentage of lactating females for NF bears were significantly greater than that of Park bears.

5. The percentage of lactating bears was significantly associated with age. Fifty-one (n = 39) of the old (≥10 yr), and 34% (n =78) of the middle-aged (5-9 yr) and 21% (n = 29) of the young (3-4 yr) females were lactating.

6. Hard mast, particularly white oak mast, was a significant predictor of reproduction. Differences in fertility between NF and Park bears likely are explained by the differences in mast in the 2 habitats.

7. The annual mortality rate for bears in the Smokies was approximately 26%. Mortality was lower for bears in the Park (22%) than for NF (30%) bears. By age group and sex, mortality rates of SM bears were largely comparable to those of bears in other studies.

8. The population estimate was 148 bears or 0.292 bears/km^2 for the Park, 28 bears or 0.350 bears/km^2 for CNF, and 24 bears or 0.211 bears/km^2 for PNF study areas. In comparison to other studies of black bears in North

America, these estimates are low to intermediate on a low-high density continuum.

9. Population and growth estimates indicated a slightly to moderately increasing population. The population estimate for the Park rose from 123 to 170 bears from the first half of the study (1972-1979) to the second half (1980-1988). The intrinsic rate of growth, r, for SM bears ranged from 2 to 11%.

10. Model simulations indicated the importance of food and consequent trends in population growth. However, weaknesses in the model were apparent and future versions should attempt to incorporate other factors which influence population growth.

11. Habitat quality is a chief factor in regulating the number of bears in the Smoky Mountains. Specifically, hard mast availability is important to female reproduction and cub survival.

12. Hunting, legal and illegal, appears to control population numbers as well, especially in the national forests. Conceivably, mortality due to hunting may, in part, explain the elevated reproductive rates of females in the national forests where harvest rates are high; if hunting can reduce the density enough so that fewer bears enjoy more habitat, then one might expect the reproductive rates of the fewer females to improve.

13. Black bear abundance in GSMNP also appears to be

determined by subadult dispersal. With increasing density, young bears in GSMNP may be forced to the Park's less-protected perimeter, where they are subjected to more hunting and poaching.

14. Disease and parasites probably have very little impact on the health of the SM bear population.

15. Protection of food (habitat) and females (whose fertility increases with age and weight) are critical to the maintenance of the SM bear population.

16. Status (wild or panhandler) and gender were significantly associated. Of the wild bear captures, 54% were males, whereas 60% ($\underline{n}$ = 209) of the panhandler captures were.

17. Panhandler females were typically young bears. The mean ages of wild (4.4 yr) and panhandler (3.2 yr) were significantly different. Lower survival among panhandlers likely contributes to their lower mean age.

18. Adult and subadult panhandlers were typically bigger and grew faster than their wild counterparts. Differences in size and growth reflect the panhandlers access to and consumption of high-energy, human-made foods.

19. Panhandler females were more fertile than wild bears. Fifty-six percent of the panhandlers were lactating, whereas only 33% of the wild females were. Improved fertility is common among panhandler bears or bears that supplement their diets with high-energy, human-

made foods.

20. Wild bears of the national forests were bigger and more fertile than Park bears. Adults in Cherokee and Pisgah National Forests were significantly heavier, and 50% of the NF and only 29% of the Park females were lactating. Differences in size and fertility of wild bears within the Smokies probably were due to differences in fall mast production; mast production in the national forests is significantly greater than that in the Park.

21. Differences in demographic characteristics between wild and panhandler bears also may reflect the effects of human-made food, the availability of which varies with panhandler bear management.

22. Measurements of the chest, neck, and total length were the best predictors of body weight.

APPENDICES

APPENDIX A

MAST DATA

Table A.1. Tennessee Wildlife Resource Agency mast data[a] collected in Blount, Sevier, Cocke, Greene, Unicoi, and Monroe counties as well as the Tellico Wildlife Management Area, Tennessee, 1973-1988.

Year	White oaks	Red oaks	White and red oaks
1973	29.56 (8)[b]	12.46 (9)	20.51 (17)
1974	15.77 (157)	8.99 (114)	12.92 (271)
1975	10.66 (85)	17.31 (104)	14.32 (189)
1976	14.60 (104)	22.53 (161)	19.42 (265)
1977	21.56 (114)	21.37 (113)	21.47 (227)
1978	11.45 (55)	11.81 (48)	11.62 (103)
1979	18.21 (106)	18.99 (79)	18.54 (185)
1980	11.14 (67)	23.24 (125)	19.02 (192)
1981	21.44 (107)	17.95 (89)	19.86 (196)
1982	9.64 (40)	16.93 (124)	15.15 (164)
1983	22.04 (81)	11.40 (63)	17.39 (144)
1984	8.74 (27)	18.54 (41)	14.65 (68)
1985	33.31 (124)	35.25 (135)	34.32 (259)
1986	14.02 (41)	7.37 (49)	10.40 (90)
1987	13.50 (73)	15.08 (89)	14.37 (162)
1988	21.42 (167)	25.74 (128)	23.29 (295)

[a]Calculated as Maximum Potential Production Index (MPPI) (Pozzanghera, 1990).

[b](_n_).

Table A.2. Tennessee Wildlife Resource Agency mast data[a] collected in Blount, Sevier, Cocke, Greene, Unicoi, and Monroe counties as well as the Tellico Wildlife Management Area, Tennessee, 1973-1988.

Year	White oaks	Red oaks	White and red oaks
1973	1.91 (22)[b]	1.73 (22)	1.82 (44)
1974	3.46 (196)	2.69 (169)	3.10 (365)
1975	3.51 (85)	4.43 (104)	4.02 (189)
1976	2.43 (165)	4.68 (165)	3.56 (330)
1977	3.28 (173)	3.63 (160)	3.45 (333)
1978	0.99 (206)	1.02 (184)	1.00 (390)
1979	2.39 (167)	2.14 (164)	2.27 (331)
1980	1.18 (199)	3.18 (180)	2.13 (3.79)
1981	3.70 (130)	3.38 (120)	3.55 (250)
1982	0.75 (170)	3.12 (169)	1.56 (339)
1983	2.68 (118)	1.58 (125)	2.11 (243)
1984	0.65 (139)	1.26 (127)	0.94 (266)
1985	2.83 (205)	3.47 (190)	3.14 (395)
1986	1.41 (101)	1.44 (105)	1.43 (206)
1987	1.45 (168)	2.00 (177)	1.73 (345)
1988	3.26 (209)	3.22 (184)	3.24 (393)

[a]Calculated as the Whitehead Index (C. J. Whitehead, oak mast yields on wildlife management areas in Tennessee,

Table A.2. Continued.

Tenn. Game and Fish, unpubl. rep., 11 pp., 1969). On a 1 - 10 scale: 0 - 2.5 = poor, 2.6 - 4.5 = fair, 4.6 - 6.5 = medium, 6.6 - 8.5 = good, 8.6 - 10 = excellent.

[b]($\underline{n}$).

Table A.3. Tennessee Wildlife Resource Agency mast data[a] collected in the Tellico Wildlife Management Area, Tennessee, 1974-1988.

Year	White oaks	Red oaks	White and red oaks
1974	22.12 (35)[b]	18.20 (44)	19.94 (79)
1975	18.06 (16)	47.83 (25)	36.21 (41)
1976	15.36 (12)	38.95 (39)	33.40 (51)
1977	40.80 (24)	57.78 (34)	50.75 (58)
1978	12.15 (11)	9.88 (24)	10.59 (35)
1979	36.56 (27)	38.29 (38)	37.57 (65)
1980	0.00 (0)	41.88 (51)	41.88 (51)
1981	30.30 (37)	27.15 (39)	28.68 (76)
1982	0.00 (0)	30.03 (52)	30.03 (52)
1983	34.87 (41)	25.05 (30)	30.72 (71)
1984	22.30 (8)	37.29 (26)	33.76 (34)
1985	46.50 (31)	54.16 (53)	51.33 (84)
1986	13.57 (12)	7.05 (19)	9.57 (31)
1987	21.43 (41)	26.83 (44)	24.23 (85)
1988	26.00 (81)	49.64 (70)	36.96 (151)

[a]Calculated as Maximum Potential Production Index (MPPI) (Pozzanghera 1990).

[b](*n*).

Table A.4. Tennessee Wildlife Resource Agency mast data[a] collected in the Tellico Wildlife Management Area, Tennessee, 1974-1988.

Year	White oaks	Red oaks	White and red oaks
1974	4.38 (40)	3.89 (54)	4.10 (94)
1975	4.06 (16)	6.24 (25)	5.39 (41)
1976	1.26 (34)	5.36 (39)	3.45 (73)
1977	4.96 (26)	5.56 (39)	5.32 (65)
1978	1.40 (30)	1.98 (42)	1.74 (72)
1979	3.82 (33)	4.23 (48)	4.06 (81)
1980	0.00 (46)	4.08 (65)	2.39 (111)
1981	3.95 (42)	3.34 (58)	3.60 (100)
1982	0.00 (40)	4.08 (62)	2.48 (102)
1983	3.91 (46)	2.00 (52)	2.90 (98)
1984	0.70 (44)	2.19 (59)	1.55 (103)
1985	3.14 (50)	4.66 (61)	3.98 (111)
1986	2.11 (19)	1.93 (28)	2.00 (47)
1987	2.54 (61)	2.82 (67)	2.69 (128)
1988	3.43 (95)	3.86 (94)	3.64 (189)

[a]Calculated as the Whitehead Index (C. J. Whitehead, oak mast yields on wildlife management areas in Tennessee, Tenn. Game and Fish, unpubl. rep., 11pp., 1969);on a 1 - 10 scale: 0 - 2.5 = poor, 2.6 - 4.5 = fair, 4.6 - 6.5 =

Table A.4. Continued.

medium, 6.6 - 8.5 = good, 8.6 - 10 = excellent.

[b]($\underline{n}$).

Table A.5. Mast data[a] collected in Great Smoky Mountains National Park, 1977-1988.

Year	White oaks	Red oaks	White and red oaks
1977	2.00 (15)[b]	23.96 (19)	14.27 (34)
1978	-	-	-
1979	12.77 (51)	19.73 (42)	15.91 (93)
1980	2.92 (7)	35.47 (54)	31.73 (61)
1981	22.46 (52)	21.66 (42)	22.10 (94)
1982	0.75 (11)	9.83 (45)	8.05 (56)
1983	8.43 (9)	2.17 (5)	6.19 (14)
1984	-	-	-
1985	27.11 (55)	17.21 (49)	22.45 (104)
1986	3.79 (67)	8.31 (84)	6.30 (151)
1987	4.76 (77)	5.88 (99)	5.39 (176)
1988	3.26 (72)	8.26 (135)	6.52 (207)

[a]Calculated as Maximum Potential Production Index (MPPI) (Pozzanghera 1990).

[b](*n*).

Table A.6. Mast data[a] collected in Great Smoky Mountains National Park, 1977-1988.

Year	White oaks	Red oaks	White and red oaks
1977	2.05 (21)[b]	3.95 (21)	3.00 (42)
1978	-	-	-
1979	3.29 (65)	2.76 (67)	3.02 (132)
1980	0.39 (46)	4.06 (67)	2.57 (113)
1981	3.80 (55)	2.07 (75)	2.80 (130)
1982	0.36 (44)	1.92 (74)	1.34 (118)
1983	2.67 (9)	1.43 (7)	2.13 (16)
1984	-	-	-
1985	2.97 (72)	2.33 (70)	2.65 (142)
1986	2.11 (74)	2.68 (91)	2.42 (165)
1987	2.69 (84)	2.80 (110)	2.75 (194)
1988	2.12 (86)	2.51 (164)	2.38 (250)

[a]Calculated as the Whitehead Index (C. J. Whitehead, oak mast yields on wildlife management areas in Tennessee, Tenn. Game and Fish, unpubl. rep., 11 pp., 1969.); on a 1 - 10 scale: 0 - 2.5 = poor, 2.6 - 4.5 = fair, 4.6 - 6.5 = medium, 6.6 - 8.5 = good, 8.6 - 10 = excellent.

[b]($\underline{n}$).

Table A.7. Mast data[a] collected in or adjacent to Harmon Den, Pisgah National Forest, 1983-1988.

Year	White oaks	Red oaks	White and red oaks
1983	1.30 (5)[b]	6.91 (13)	5.35 (18)
1984	9.01 (3)	21.37 (38)	20.47 (41)
1985	7.00 (14)	26.53 (43)	21.73 (57)
1986	0.00 (2)	0.19 (14)	0.17 (16)
1987	9.11 (9)	2.66 (7)	6.29 (16)
1988	6.35 (21)	12.66 (63)	11.08 (84)

[a]Calculated as the Maximum Potential Production Index (MPPI) (Pozzanghera 1990).

[b](n).

Table A.8. Mast data[a] collected in or adjacent to Harmon Den, Pisgah National Forest, 1983-1988.

Year	White oaks	Red oaks	White and red oaks
1983	2.93 (14)[b]	3.11 (27)	3.05 (41)
1984	0.25 (36)	2.76 (63)	1.85 (99)
1985	0.97 (38)	3.31 (54)	2.34 (92)
1986	0.00 (18)	0.28 (58)	0.22 (86)
1987	0.85 (33)	0.28 (58)	0.49 (91)
1988	2.24 (29)	3.49 (68)	3.12 (97)

[a]Calculated as the Whitehead Index (C. J. Whitehead, oak mast yields on wildlife management areas in Tennessee, Tenn. Game and Fish, unpubl. rep., 11pp., 1969; on a 1 - 10 scale: 0 - 2.5 = poor, 2.6 - 4.5 = fair, 4.6 - 6.5 = medium, 6.6 - 8.5 = good, 8.6 - 10 = excellent.

[b]($\underline{n}$).

APPENDIX B

LIFE HISTORY DATA

Table B.1. Life history characteristics of female black bears in Great Smoky Mountains National Park, 1972-1989, used in BEAR (Mathis et al. 1990), a population model.

Age class	N[a]	Survivorship Rate (P_x)	Fecundity Rate (m_x)[b]
0.5	70	0.545	0.000
1.5	38	0.880	0.000
2.5	33	0.864	0.000
3.5	29	0.852	0.500
4.5	25	0.847	0.428
5.5	21	0.832	0.360
6.5	18	0.828	0.464
7.5	14	0.811	0.479
8.5	12	0.811	0.536
9.5	10	0.794	0.500
10.5	8	0.793	0.500
11.5	6	0.783	0.500
12.5	5	0.778	0.542
13.5	4	0.750	0.500
14.5	3	0.762	0.562
15.5[c]	1	0.750	0.643

[a]Based on a total population of 592 bears.

[b]No. female young per adult female per year.

[c]Mean values of female bears ≥15 yr.

Table B.2. Life history characteristics of female black bears in Cherokee and Pisgah National Forests, 1978-1989, used in BEAR (Mathis et al. 1990), a population model.

Age class	N[a]	Survivorship Rate (P_x)	Fecundity Rate (m_x)[b]
0.5	4	0.952	0.000
1.5	3	0.842	0.000
2.5	3	0.821	0.000
3.5	3	0.798	0.625
4.5	2	0.774	0.469
5.5	1	0.758	0.500
6.5	1	0.753	0.333
7.5	1	0.724	0.562
8.5	1	0.709	1.000
9.5	1	0.688	0.750
10.5	1	0.375	0.690

[a]Based on a total population of about 40 bears.

[b]No. female young per adult female per year.

[c]Mean values of female bears ≥10 yr.

VITA

The son of Peggy and Copley McLean, Peter Kleppinger McLean was born and raised in Charlottesville, Virginia where, in 1974, he was graduated from Lane High School. Peter attended the University of Virginia where he majored in environmental science and minored in history. In May of 1978, he was graduated from the University and, that fall, taught biology and American history at the Virginia Episcopal School in Lynchburg, Virginia.

After working as a seasonal ranger in Yellowstone National Park and an admission's officer at Randolph-Macon Woman's College, Peter entered the master's degree program in biology at the College of William and Mary. There, he studied the feeding behavior of ospreys on the Chesapeake Bay and was graduated in 1986.

Peter began his doctoral work on the black bears in the Smoky Mountains the summer of 1986 and received the Doctor of Philosophy degree, with a major in ecology, the spring of 1991.